Sexual dimorphism and alternative reproductive tactics in the Midland Painted Turtle (*Chrysemys picta marginata*)

by

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Abstract

The reproductive strategy of Painted Turtles (*Chrysemys picta*) has been described as a combination of male courtship and female mate choice. However, *in situ* field observations from a long-term study of *C. picta* in Algonquin Provincial Park (Ontario, Canada) suggest that males also demonstrate coercive mating tactics. Males are equipped with prominent tomiodonts, tooth-like cusps of the upper jaw, which seemingly function in restraining mates and result in wounding to the head and neck of females. I propose that the tomiodonts of male *C. picta* serve as sexual weapons used to coerce females into mating. This thesis has two main objectives: 1) to describe the tomiodont morphology of *C. picta*, and 2) to test the functional significance of tomiodonts in the mating tactics of male *C. picta*. In Chapter I, I investigate the overall cranial morphology of *C. picta* with an emphasis on sexual dimorphism of the tomiodonts. I show that male *C. picta* have sexually size dimorphic tomiodonts with an optimized arrangement for biting and gripping. In Chapter II, I investigate the soft tissue wounding demographics of a *C. picta* population as these wounds relate to antagonistic sexual interactions. Using a 24-year dataset on wounding I show that large females experience the highest wounding probability and that elevated rates of wounding occur during the late summer breeding period. In Chapter III, I use behavioural trials during the spring and late summer reproductive seasons to evaluate male reproductive behaviour. I show that small males court females through titillation, whereas larger males employ coercive tactics, such as biting and forced submergence. My findings are contrary to the female choice mating system reported for *C. picta* and join a growing body of research demonstrating the importance of coercive tactics in the reproduction of male emydid turtles.

functional morphology, comparative morphology, sexual dimorphism, animal behaviour, animal reproduction, sexual conflict, sexual behaviour, herpetology, freshwater turtle, natural history.

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"*There's no simple*
Explanation
For anything important
Any of us do"

Gord Downie, The Tragically Hip
"Courage (for Hugh MacLennan)", Fully Completely (1992)

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Sexual dimorphism and alternative reproductive tactics in the Midland Painted Turtle (*Chrysemys picta marginata*)

General Introduction

Background

The Painted Turtle (*Chrysemys picta*) is among the most conspicuous of North American turtles. Owing to its large geographic range, gregarious basking congregations, convenient size, and adornment of bright colours and intricate patterns on the head, neck and limbs, this species has long attracted the attention of naturalists, biologists, and the public. Today *Chrysemys* is among the most well-studied turtles of North America (Lovich and Ennen 2013) and, arguably, the world. Despite a long history of observation and scientific endeavour related to *Chrysemys,* many facets of its basic biology still remain unknown. Among these poorly understood aspects is the mating system of *C. picta*.

Sexual dimorphism in chelonians

Sexually dimorphic traits are common in chelonians and often reflect the challenges associated with mating, such as male mounting and/or the maintenance of a secure copulatory position (Figure 0.1). Sexual shape dimorphism is regularly observed among terrestrial and aquatic chelonians. Males often demonstrate a concavity of the plastron that aids in mounting the domed carapace of the female. It has been suggested that the relatively high carapace of females is an adaptation to increase the internal body volume for accommodating eggs (Muñoz and Nicolau 2006, Kaddour *et al*. 2008, Bonnet *et al*. 2010, Lui *et al*. 2013); and indeed larger female *C. picta* are more fecund

(McTaggart 2000, Mcguire *et al*. 2008), a quality that may make them more attractive as mates (Pearce *et al*. 2002, McGuire *et al*. 2008). Males have larger shell openings, notably in the inguinal region, enhancing limb and tail mobility, aiding in copulation at the expense of protection (Muñoz and Nicolau 2006, Bonnet *et al*. 2010). To house the penis, male chelonians generally possess a longer tail and wider tail base than do females.

Both male- and female-biased sexual size dimorphisms are well-recorded in chelonians and have been related to male mating strategies, female fecundity, ecological selection and phylogenetic patterns (Berry and Shine 1980, Shine 1989, Stephens and Wiens 2009, Liu *et al*. 2013). Interestingly, members of Emydidae (*e.g*., *Graptemys*) rank among the most extreme cases of sexual size dimorphism known in tetrapods (Stephens and Wiens 2009).

Among tortoises, the gular scute(s) may form a projection that extends anteriorly from the plastron. These projections may be pronged, as in Gopher Tortoises (*Gopherus* spp.: Auffenberg 1966, McRae *et al*. 1981) and the African Spurred Tortoise (*Geochelone sulcata*; Ernst *et al*. 2008, Pellett and Cope 2013), or a single spade-like projection, as in the Angulate Tortoise (*Chersina angulate*; Ven den Berg 1994, Mann *et al*. 2006). Males use their projecting gulars as an intrasexual weapon to ram opponents during sparring bouts over territory or for access to mates (Miller 1955, Douglass 1976, Douglass and Layne 1978, McRae *et al*. 1981, Branch 1984, Bonnet *et al*. 2001, Mann *et al*. 2006). In some species, the gular may also be used to ram females during courtship (Auffenburg 1966, Branch 1984).

Modifications of the forelimb and hindlimb claws occur in North American pond turtles (Emydidae). Elongate forelimb claws used in elaborate tactile courtship displays

are seen in males of numerous taxa (*Chrysemys*, *Pseudemys*, *Trachemys* and some *Graptemys*). Darwin (1871, citing Maynard 1869) remarks, "The male of the mud-turtle of the United States (*Chrysemys picta*) has claws on his front feet twice as long as those of the female; and these are used when the sexes unite." In addition, male Box Turtles (*Terrapene*) demonstrate recurved claws on the hindfeet to maintain a secure grip on the female during copulation (Cahn and Conder 1932, Evans 1951, 1953). It has also been suggested that male Box Turtles employ their recurved claw as a sexual stimulus by scratching the posterior-lateral carapace of females following mounting (Evans 1953). Some male Sea Turtles are equipped with hook-like claws on the anterior flippers (Prichard and Mortimer 1999) to aid in gripping the female's carapace during mating (Booth and Peters 1972, Comuzzie and Owens 1990).

Secondary sexual structures are also present as modifications to soft tissue. Male Mud and Musk Turtles (Kinosteridae) have a rough patch of skin on the inner hindlimb that is used maintain a secure mounted position and/or grip the tail of the female during coitus (Mahmoud 1967, Berry and Shine 1980, Ernst and Lovich 2009). Male kinosternids also possess a spur on the tip of the tail that prods the female during mating (Mahmoud 1967). Striking dichromatisms have been described seasonally and sexually for chelonian species. Perhaps the most extreme example is the Painted Terrapin (*Callagur borneoensis*) in which males adopt a white-pink head colour with a brilliant red, dorsal head stripe during the breeding season (Moll *et al*. 1981). Changes in colouration to the head and soft skin are also recorded for the Forsten's Tortoise (*Indotestudo forstenii*) and Elongated Tortoise (*I. elongata*) (Moll *et al*. 1981). An ontogenetic sexual dichromatism in the form of melanism is pronounced in older or

larger male Yellow-bellied Sliders, *Trachemys scripta* (Lovich *et al*. 1990, Tucker *et al*. 1995).

Cranial sexual dimorphism in emydid turtles

In a number of North American turtle species there is a pronounced sexual dimorphism in head size, notably among the Map Turtles and Sawbacks (*Graptemys* spp.; Bertl and Killebrew 1983, Lindeman 2000, 2006) and Cooters and Red-bellied Turtles (*Pseudemys* spp.; Bever 2008, 2009). Additionally, head width is sexually dimorphic in the Wood Turtle, *Glyptemys insulpta* (Greaves and Litzgus 2009). These differences in head size are commonly attributed to dietary partitioning, among other ecological pressures (Shine 1989, Stephens and Wiens 2009, Underwood *et al*. 2013).

Another taxonomically diverse group of turtles, the Sliders (*Trachemys* spp.), represent an interesting group in which to explore sexual differences in head morphology. All slider subspecies from the United States (*elegans*, *scripta* and *troosti*) share three derived characters: males possess elongated foreclaws, an elaborate male titillation courtship display making use of the exaggerated claws, and a female-biased sexual size dimorphism (Gibbons and Lovich 1990, Legler 1990). In temperate species and subspecies of *Trachemys* from the United States, there is no apparent sexual dimorphism in snout length (Seidel 2002, Legler and Vogt 2013). Among Antillean *Trachemys* there are slight but constant differences in shape and proportions of the snout (Barbour and Carr 1940). Further, sexual differences in snout length of Antillean *Trachemys* have lead to taxonomic confusion (Barbour and Carr 1940). Males of the *Trachemys stejnegeri* group of the West Indies demonstrate a snout that is notably extended, upturned, and with

an anterior surface that is "sharply retreating" (Barbour and Carr 1940). A gradient of snout morphology characters exists among males of numerous Mexican *Trachemys* subspecies. The degree of elongation, pointedness and upturning of the snout is reportedly absent in *elegans* and *taylori*; noticeable in *gaigeae*, *hartwegi*, *yaquia*, and *ornata*; and extreme in *venusta*, *cataspila*, *grayi*, *nebulosa*, and *hiltoni* (Figure 0.2; Legler and Vogt 2013, also see Seidel 2002). For old, large males (note that the distinction between age and size is not made by the authors) belonging to the latter "extreme" taxa, a dramatic reshaping of the skull takes place involving the thickening and upturning of the prefrontal bones and enlargement of the maxillaries and premaxillaries (Figure 0.3; Legler and Vogt 2013). In *T. s. hiltoni* the enlargement of the snout in mature males is reported to progress with age (Legler and Vogt 2013). This results in a bulbous, bosslike modification of the snout that gives individuals a very distinctive head profile (Legler and Vogt 2013). Multiple references to intersexual differences in head shape are made in the taxonomic evaluation of *Trachemys venusta* (McCord *et al*. 2010). For instance, the snout of *T. v. grayi* is recognized as more protuberant in males than females, and in male *T. v. uhrigi* the snout is more pointed than that of females. The cranial dimorphism is so striking in Panamian *Trachemys scripta* that adult males and females can be distinguished at distances up to 100 m (with the aid of binoculars) based on head shape alone (Moll and Legler 1971). Legler and Moll (1971) note that elongation of the foreclaws and/or snout in male *Chrysemys* and *Pseudemys* (=*Trachemys*) ranges from mildly expressed (*i.e.*, not noticeably but statistically demonstrable) to spectacular. It has been hypothesized that the selective forces acting on the foreclaw and snout phenotypes differ, perhaps due to emydine species sympatry, between the United States and Mesoamerican Sliders (Legler

1990, Legler and Vogt 2013). Little functional significance has been ascribed to the elongate snout of males other than its possible role in mating (Legler and Moll 1971). More recently it has been proposed that the elongated snout may act in mate recognition or serve as an "erotic prod" (Legler 1990, Legler and Vogt 2013). Despite interest in the highly variable cranial morphology between male and female *Trachemys*, the abovementioned dimorphic traits (specifically snout length) have only been quantified in one previous study (Seidel *et al*. 1999).

Patterns of sexual dimorphism and courtship in Trachemys

The character trait differences within temperate and tropical *Trachemys* are not restricted to head morphology. Mature males of all three U.S. *Trachemys* subspecies and Antillean *Trachemys* species possess elongated foreclaws and a smaller body size relative to females (Seidel 2002, Ernst and Lovich 2009). By contrast, elongate foreclaws are rare and irregular in Mesoamerican *Trachemys* and males and females are approximately equal in size (Figure 0.4; Gibbons and Lovich 1990, Legler 1990, Leger and Vogt 2013), suggesting a biogeographic pattern in this secondary sexual trait. Mature male *Trachemys scripta* subspecies of Panamá do not possess noticeably elongate forelimb claws, although their snout is elongated and upturned (Moll and Legler 1971). In the character matrix developed by Seidel (2002) for a taxonomic review of extant *Trachemys*, it is clearly shown that *Trachemys* with the most extreme snout elongation lack elongate foreclaws (also see Leger and Vogt 2013).

Interestingly, multiple workers have reported that foreclaw and snout elongation are related to dichotomous reproductive patterns (Rosado 1967, Moll and Leger 1971,

Medem 1975, Legler 1990, Moll and Moll 1990, Seidel 2002, Legler and Vogt 2013). That is, either the presence or absence of titillation co-varies with the presence of elongated foreclaws or elongate snout in males, respectively. The short-snouted and long-clawed male *Trachemys* of the United States demonstrate an elaborate titillation courtship display. Conversely, there is little evidence that the long-snouted and short-clawed Central American *Trachemys scripta* demonstrate elaborate courtship displays like their northern conspecifics. Observations collected by Moll and Legler (1971) suggest that Panamanian male *Trachemys* pursue a female and mount her carapace with no beforehand foreclaw display. Similar observations are reported for the longer snouted taxa *venusta*, *hiltoni*, *gaigae*, *callirostris* and *dorbigni*. Rosado (1967) describes courtship in captive Mexican sliders (*T*. *o*. *ornata* and *T*. *grayi*), although the pre-copulatory displays do not involve titillation. Rather, males eject a stream of water from their nostrils, as has been reported in other turtle taxa (Liu *et al*. 2013). Water squirting behaviour has also been observed outside of reproduction in *T*. *scripta*, such as during feeding and surfacing to breathe, so this behaviour may not be reflective of a courtship-specific behaviour (Moll and Legler 1971). There is little evidence to suggest that elaborate courtship displays exist in tropical *Trachemys* that lack elongate foreclaws (Moll and Legler 1971, Legler 1990, Moll and Moll 1990, Seidel 2002, Legler and Vogt 2013). In short, within the closely allied genera *Trachemys*, *Pseudemys* and *Chrysemys*, there is no record of titillation behaviour in taxa that lack elongate foreclaws (Legler 1990, Legler and Vogt 2013).

Taken in combination, the elongate foreclaws, sexual size dimorphism, and elaborate courtship display may act as reproductive isolating mechanisms. This is consistent with

the presence of these traits in U.S. *Trachemys* that occur in sympatry with other closely related species, and absence of these traits in the south where most *Trachemys* occur in isolation (Figure 0.4; Legler 1990).

Sexual dimorphism in Chrysemys

Painted turtles (*Chrysemys picta*) are closely related to Cooters (*Pseudemys*) and Sliders (*Trachemys*) and are collectively recognized as pond turtles (Emydidae) (Seidel and Smith 1986, Stephens and Wiens 2003, 2009). Numerous sexual dimorphisms have been formally described for the Painted Turtle, including a larger female body size, a greater female carapace height, elongate male forelimb claws and larger male pre-cloacal tail length (Ernst and Lovich 2009). Observational evidence (M. Keevil, J. Riley and P. Moldowan, pers obs.) from a long-term study of Painted Turtles in Algonquin Provincial Park, ON, Canada, has suggested that a cranial sexual dimorphism may exist. Most notably there appears to be variation in rostrum length, tomiodont morphology (discussed below) and overall head shape between the sexes (Figure 0.5, Figure 0.6). Presently, no attention has been given to potential intersexual differences in head shape and structure, or to their functional significance, in *C. picta*.

The turtles with "teeth"

Painted turtles possess a bicuspid tooth-like structure medial on the upper jawline that borders a "V"-shaped notch in the pre-maxillary bone (Figure 0.6, Figure 0.7). These "teeth", "cusps", or "protuberances", as they have been described in the literature (Appendix I, Table A1.1), are most appropriately termed tomiodonts, from the Greek

derivation of "*tomy*" meaning a sharp or cutting edge and "*dont*" meaning tooth. Minx (1996) appears to be the first to have published the term tomiodont in the formal literature, although he credits the late Arnold B. Grobman (1918-2012, Chancellor Emeritus and Research Professor, University of Missouri), his thesis supervisor, for use of the name (Minx, pers. comm. 2014). Tomiodont was first used to describe the variation in upper jawline structure of box turtles (Testudines: Emydidae: *Terrapene*) for the purpose of phylogenetics. Species with an apical tip to their beak (*e.g.*, *Terrapene carolina carolina*) are described as having a single tomiodont. Other taxa may have a bicuspid beak or two tomiodonts, arranged such that a single tomiodont flanks either side of a shallow or deep premaxillary notch (*e.g.*, *Terrapene nelsoni*, *T. coahuila*, *T. c. ornata*) (Minx 1996). It is relevant to note that the term "tomium" is used in the literature to describe the cutting or biting edge of the beak in turtles (*e.g.*, Gaffney 1979, Broadley 1981, Pritchard and Mortimer 1999) and birds (*e.g.*, Proctor and Lynch 1993, Feduccia 1999, Greenberg *et al*. 2013) and "tomial teeth" are described in Falconidae and other predatory birds (Proctor and Lynch 1993, Hartel 1995, Csermely *et al*. 1998, Fowler *et al*. 2009). The shared etymological origins of the word can be seen in taxonomy, such as the genus *Tomiostoma*, the very toothy false gharials.

Tomiodonts, by one description or another, have been used as a defining character for *Chrysemys* in a variety of sources across numerous disciplines (Appendix I, Table A1.2). For example, the tomiodonts have been used as an anatomical landmark in descriptions of cranial morphology. Early taxonomic classification and natural history descriptions from the mid-1800s (see Holbrook 1836-1840, De Kay 1942, and Agassiz 1857) have included these structures. Many natural historians have also illustrated

tomiodonts in plate drawings (Appendix I). Today, tomiodonts are still used as a descriptor in taxonomy and phylogenetics (Seidel and Jackson 1990, Siedel 2002, Stephens and Wiens 2003), reference books on turtle biology (Jensen *et al*. 2008, Ernst and Lovich 2009, Legler and Vogt 2013) and field guides (Harding 1997, Sheldon 2006). Despite the widespread description of tomiodonts (under numerous synonymous names; Appendix I, Table A1.2) spanning nearly 180 years, no effort has been made to quantitatively evaluate these structures in *Chrysemys* or any other taxa.

The osteological origin, development and general form of tomiodonts have seemingly not been addressed in texts addressing chelonian skull anatomy, although the premaxillary notch is recorded with regularity. It appears that the median premaxillary notch and associated tomiodonts are features of the premaxillary bone, at least in *C. picta* (Figure 0.7). This would suggest that the tomiodonts are of dermal bone origin, at least in part, rather than simply an artefact of the keratinized beak that overlies the triturating surface of the premaxillary.

The tomiodonts of males in some *Terrapene* sp. may be more pronounced compared to females (Minx 1996). Further, it is recognized that the pre-maxillary notch wears smooth with age, suggesting that the examination of juveniles is important for evaluating this character (Minx 1996). Tomiodonts are prominent jawline features in the Alabama Red-bellied Cooter (*Pseudemys alabamensis*) occurring ubiquitously in both sexes, and observable in hatchlings (D. Nelson, pers. comm. 2014). The term tomiodont appears to have received little direct attention in the literature, only appearing on one other occasion to describe the jawline structure of *Actinemys*, *Clemmys* and *Glyptemys* (Emydidae) (Holman and Fritz 2001). In other cases, tomidonts have been referred to as

"teeth", "cusps", "protuberances", "processes", "projections", or the jawline as "dentate", *et cetera* (Appendix I, Table A1.1). Bicuspid tomiodonts are seen in a few other members of the family Emydidae, including *Pseudemys* and *Rhinoclemmys*, as well as in other taxonomically diverse turtle species (Appendix I, Table A1.2).

Observations of male tomiodont variation, female wounding, and male-female antagonism

In the long-term study of Painted Turtles at the Arowhon sites in Algonquin Provincial Park (initiated in 1978, R.J. Brooks, University of Guelph) there is a record as early as 1993 referring to turtles possessing "fangs" or with "vampire teeth". In all, there were 14 observations making reference to six individuals for which these features are described. In all cases these individuals were male. Continued observational study of Algonquin Provincial Park Painted Turtles in 2010 and 2011 suggested that males from multiple populations had prominent tomiodonts of variable morphology, whereas females usually had less variable and less prominent tomidonts (Figure 0.6; M. Keevil, J. Riley and P. Moldowan, pers obs.). The putatively sexually dimorphic nature of the tomiodonts raised a number of questions about their possible functional significance. The Algonquin Park long-term study offered another unique set of observations. Researchers were documenting regular soft tissue wounding in reproductive female *C. picta*, principally wounds on the head and neck inflicted by conspecifics. The origin and, again, significance of these wounds was unclear. Field researchers slowly began accumulating *in situ* observations of male-female antagonism while sampling. Male *C. picta* were observed striking and biting females. The overtly aggressive behaviours of male *C. picta*

seemed to be in a reproductive context, given that the *in situ* observations and wounding disproportionately involved females. Such behaviour appeared contradictory to the present state of knowledge on *C. picta* reproductive tactics, which are widely recognized as involving a rather amorous male foreclaw courtship display known as titillation. Why would males direct coercive behaviours toward females? Was the wounding observed on females a result of male aggression? What can be said of the putative tomiodont dimorphism? This collection of observations and questions cumulated to form this thesis project on sexual dimorphism and alternative reproductive tactics in *C. picta*.

Project direction

In Chapter I, I investigate the overall cranial morphology of the Midland Painted Turtle (*C. p. marginata*) with an emphasis on sexual dimorphism of the tomiodonts. Chapter I provides the underlying framework on which to discuss the functional significance of tomiodonts, the origin of female wounds (Chapter II), and how the tomiodonts relate to the mating tactics of *C. p. marginata* (Chapter III).

In Chapter II, I investigate the soft tissue wounding demographics of the long-term Arowhon *C. picta* population as these wounds relate to the antagonistic interactions between males and females.

In Chapter III, I use behavioural trials during the spring and late summer reproductive seasons to evaluate male reproductive behaviour and unite evidence of a male tomiodont dimorphism and female-biased wounding patterns.

Rationale

The Painted Turtle is a model species, recognized for its contribution to studies ranging from developmental biology to overwintering physiology, and growing involvement in genetics, genomics, and biomedical research (Valenzuela 2009). Compared to most other turtle species, the life history of the Painted Turtle is well-studied and can be used to address questions related to their evolution and ecology. Wolf Howl Pond and West Rose Lake, the Arowhon sites in Algonquin Park, are an ideal system in which to study the reproductive biology of *C. picta* owing to the well-established life-history study of the species, ongoing since 1978. Previous investigators have addressed aspects of reproductive biology, including sex ratio, sexual dimorphism, reproductive behaviour, mate choice, reproductive success, and paternity, at the Arowhon sites. My research builds on the knowledge of these past studies. By integrating morphology and behaviour, my research has application in the study of life-history evolution. As a group with a rich evolutionary history, emydid turtles are a fascinating taxon in which to ask questions about mating system evolution. My study also addresses the importance of secondary sexual traits in mating strategies and the role of sexual selection in the development of sexual dimorphisms and variation in male phenotype.

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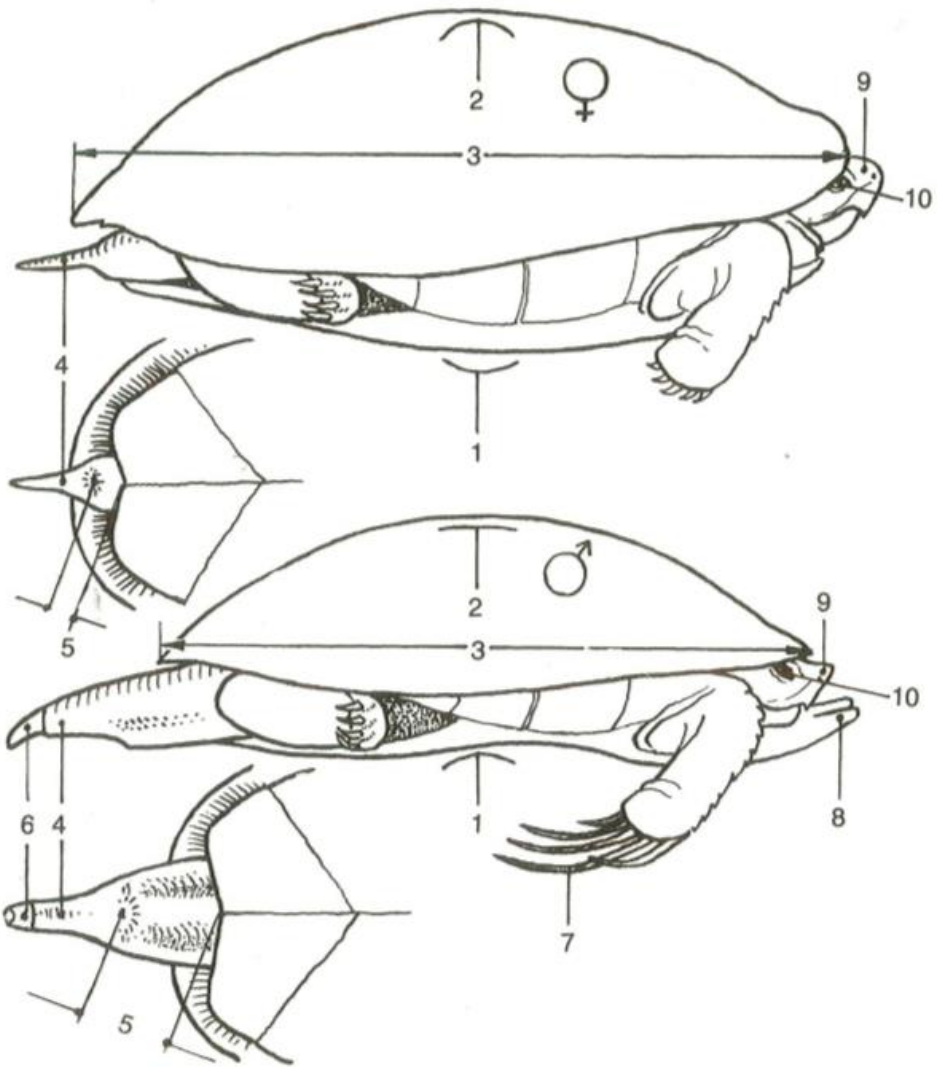

Figure 0.1: Sexual dimorphisms in turtles. 1. Curvature of the plastron: flat or convex in female, concave in male; 2. Curvature of the carapace: in female the carapace is more steeply curved and with a greater absolute shell height, in males the carapace is flatter with a smaller absolute height; 3. Differences in total shell length (both carapace and plastron), mostly favouring a larger female size; 4. Form and length of tail: greater absolute length and thickness in the tails of male; 5. Distance between cloaca and posterior edge of plastron: greater absolutely pre-cloacal tail length of male; 6. Keratinized spur on tail tip absent or subtle in females, pronounced in males; 7. Elongated foreclaws in male; 8. Elongated gular scutes that form a ramming projection in male (tortoises); 9. Extension of the snout in males (pond turtles, Emydidae); 10. Vibrant iris (eye) colour in males (pond turtles, Emydidae). Diagrams do not show all known secondary sexual traits in turtles, nor do all the illustrated traits occur in a single species or group. (Text and illustration from Obst 1988.)

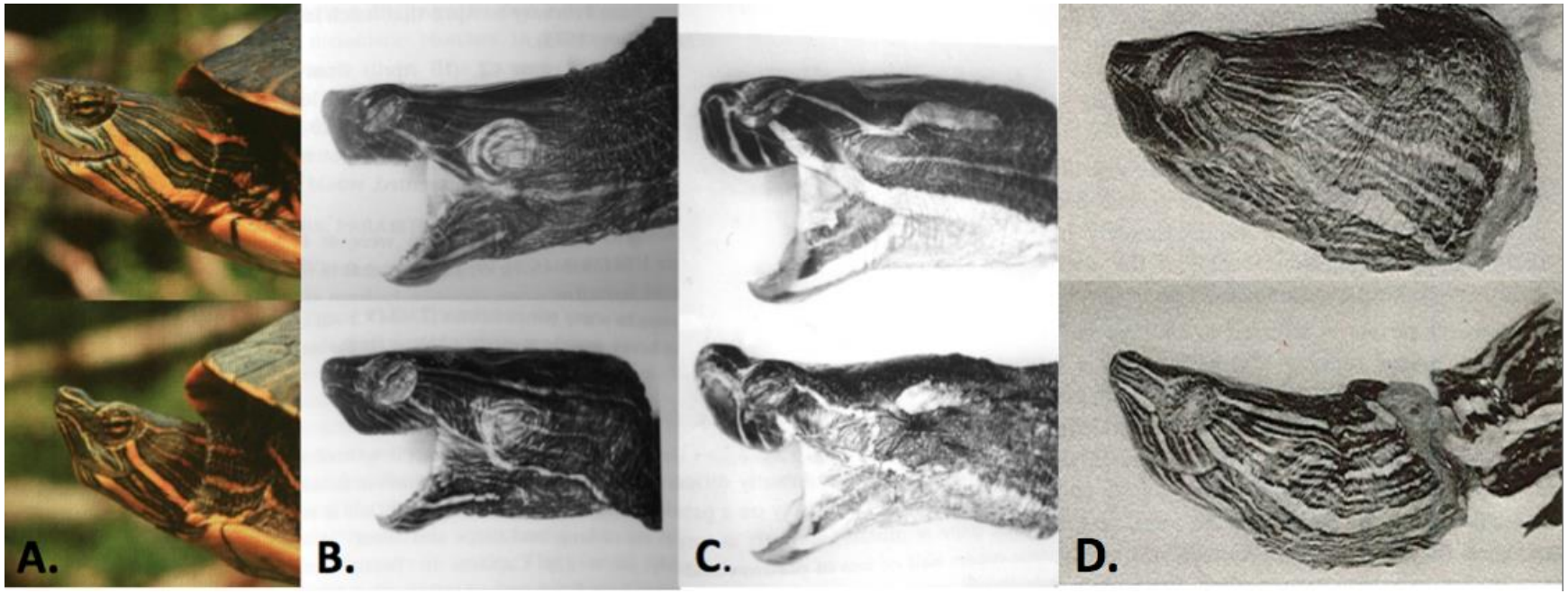

Figure 0.2: Sexual dimorphism in cranial structure of *Trachemys* spp. A. *Trachemys scripta venusta*, female (top) and male (bottom). B. *Trachemys scripta grayi*, female (top) and male (bottom). C. *Trachemys scripta hiltoni*, female (top) and male (bottom). D. *Trachemys scripta* from Juan Mina, Canal Zone, Panamá, female (top) and male (bottom) (Text and illustrations A-C from Legler and Vogt 2013, illustration D from Legler 1990).

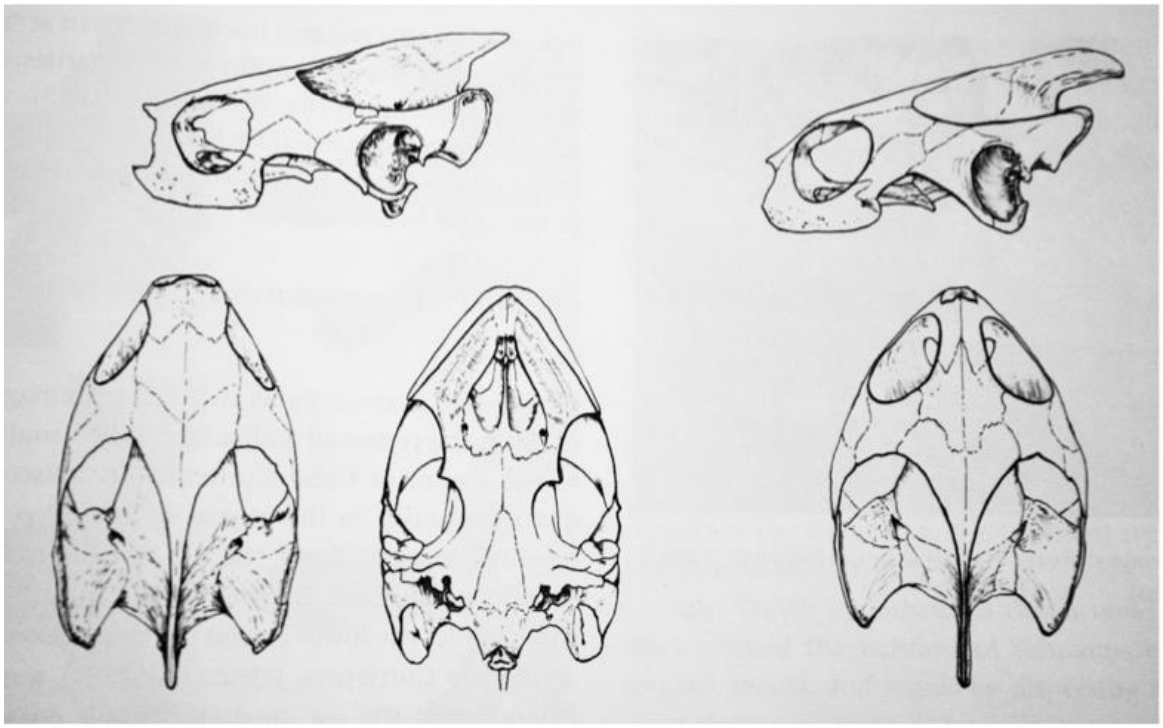

Figure 0.3: Skulls of two subspecies of *Trachemys scripta*. Left – *T*. *s*. *hiltoni*, adult male in lateral, dorsal, and ventral view; right – *T*. *s*. *ornata*, adult male in lateral an dorsal view. Note profile of snout region. Older male *T*. *s*. *hiltoni* may demonstrate an extreme bulbous, bosslike modification of the snout. In contrast, this trait is subtle, if present at all, in *T*. *s*. *ornata*. Skulls shown at same size for comparison (Illustration from Legler and Vogt 2013).

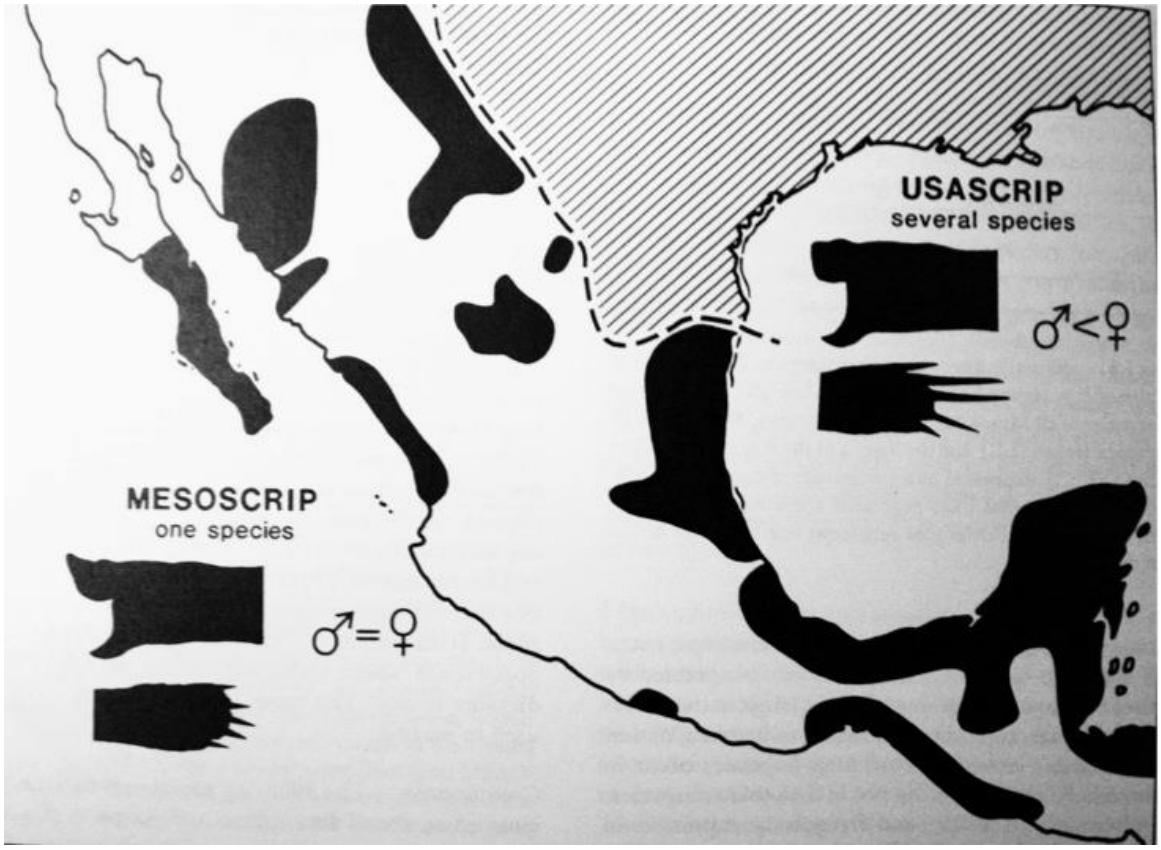

Figure 0.4: Map showing the distribution of Mexican *Trachemys* species (MESOSCRIPT). The diagonally shaded area indicates where more than one species of *Trachemys* (USASCRIP) occurs. South and west of the Rio Grande, *Trachemys scripta* is the only emydid turtle (solid black). In the area of sympatry, males are smaller than females, lack a pointed snout, and have elongated foreclaws and demonstrate an elaborate stereotypic courtship display. In the area of non-sympatry, males are about the same size as females, have a pointed snout, lack the elongated foreclaws and do not display to females during courtship (Illustration and text, Legler 1990).

Figure 0.5: Lateral head photographs of female (left) and male (right) Midland Painted Turtle (*Chrysemys picta marginata*) from the well-studied Arowhon population, Algonquin Provincial Park (Ontario, Canada). Note the relatively longer and anteriorly tapering (pointed) rostrum of the male. The head of the female demonstrates a comparatively blunt rostrum, a sloping forehead (orbital-rostrum region), and an overall more stocky build.

Figure 0.6: Intrasexual variation in male Midland Painted Turtle (*Chrysemys picta marginata*) tomiodont morphology from Algonquin Provincial Park (Ontario, Canada). Note on the left the larger and more prominent tomiodonts (at arrowhead) compared to that of the individual on the right.

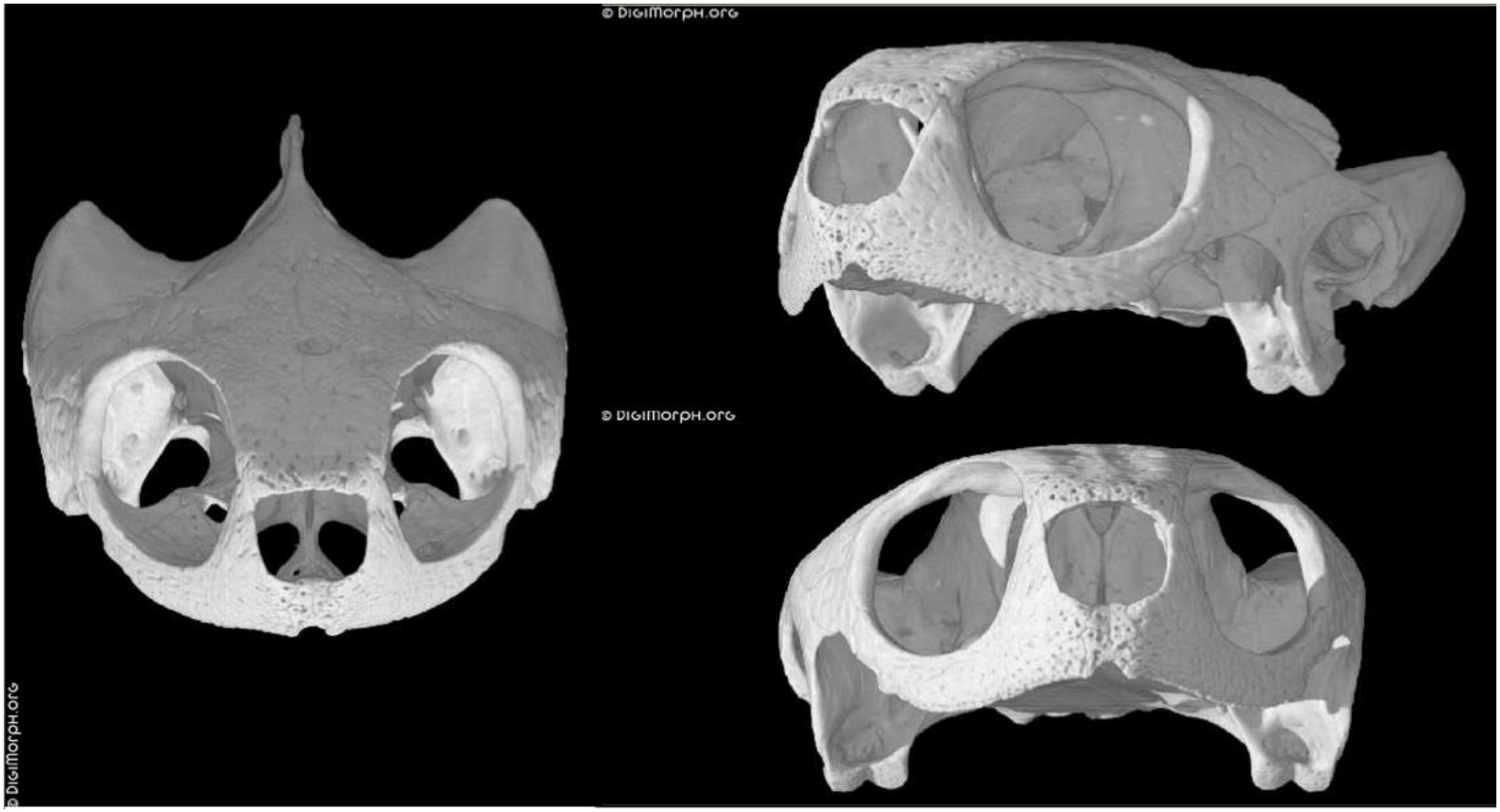

Figure 0.7: Frontal images of the Painted Turtle (*Chrysemys picta*) skull demonstrating the premaxillary notch and bicuspid tomiodonts. Sex of specimen unknown. Images courtesy the Digital Morphology library (2014) <http://digimorph.org/>.

Chapter I

Head morphology, tomiodont characterization and sexual dimorphism in the Midland Painted Turtle (*Chrysemys picta marginata*)

O, be some other name!
What's in a name?
That which we call a rose (or a tomiodont)
By any other name would smell as sweet (or be as interesting).

Romeo and Juliet (II, ii, 1-2)
William Shakespeare

"*The head is moderately large and elongated; the snout pointed*. *The upper jaw is furnished in front with two remarkable teeth, and the lower has a well developed hook."*

J.E. Holbrook, in reference to a male *Chrysemys picta bellii*
North American Herpetology, Vol. 2, p. 10, 1836-1840.

Chapter I: Head morphology, tomiodont characterization and sexual dimorphism in the Midland Painted Turtle (*Chrysemys picta marginata*)

Abstract: Sexually dimorphic characters are relatively common among vertebrates and are particularly well-represented among emydid turtles. The Painted Turtle (*Chrysemys picta*) has an upper jaw notch bordered on each side by tooth-like cusps called tomiodonts. For 180 years, these tomiodonts have been used as a descriptor in chelonian anatomy, phylogenetics, and natural history; however, no quantitative study of these traits or their function has ever been completed. Observations of *C. picta* from a long-term study in Algonquin Provincial Park (Ontario, Canada) have suggested that males have tomiodonts of more variable morphology and greater prominence than those of females. I show that the head morphology of male and female *C. picta* differs notably, especially with respect to the tomiodonts. Male *C. picta* have a relatively longer head and rostrum (among other traits), giving their head a more angular appearance in lateral profile. Dietary partitioning and reproductive role hypotheses were proposed (although not explicitly tested) and tentatively dismissed, as they do not appear to explain the observed head dimorphism. I instead propose a sexual selection hypothesis, suggesting that the tomiodonts of male *C. picta* function as sexual weapons used to coerce females into mating. The tomiodont morphology of males reflects an optimized biomechanical arrangement, ideal for bite force generation and maintaining an effective biting grip. Lastly, I suggest an additional novel dimorphism of the male *C. picta* anterior carapace, namely the serrated anterior marginal scutes and projecting nuchal scute, whose functional significance warrants further study.

Introduction

Sexually dimorphic characters are relatively common among vertebrates, ranging from dramatic body size disparities to more subtle differences in morphology. The mechanism(s) driving the evolution of sexual dimorphism is dependent upon species' biology and the dimorphic trait in question. Among the many hypotheses proposed to explain the evolution of sexual dimorphisms, three have been given the bulk of attention: (1) sexual selection, attributable to variation in mating success; (2) fecundity selection, which favours a large female body size when there is a positive relationship between offspring number and/or offspring size and maternal size; and (3) natural selection, arising from reproductive roles and/or resource partitioning between the sexes (Cox *et al*. 2008). Reptiles have been featured prominently in research on sexual dimorphism

because of their high degree of variation in dimorphisms and life histories (Cox *et al*. 2008). Turtles, specifically members of Emydidae, have been of particular interest because they exhibit a considerable range of sexual dimorphisms (Figure 0.1) and have been subject to relatively thorough ecological study (Stephens and Wiens 2009).

Several sexual dimorphisms have been described for the Painted Turtle (*Chrysemys picta*: Emydidae), including larger female body size, greater female carapace height, elongate male forelimb claws and larger male pre-cloacal tail length (Ernst and Lovich 2009). During breeding, males actively participate in a courtship display known as titillation, by stroking the female with their lengthy forelimb claws (Taylor 1933, Cagle 1954, Ernst 1971, Berry and Shine 1980, Ernst and Lovich 2009). Observational evidence (M. Keevil, J. Riley and P. Moldowan, pers obs.) from a long-term study of Painted Turtles in Algonquin Provincial Park, ON, Canada (*ca*. R.J. Brooks 1978), has suggested that a sexual dimorphism may exist in *C*. *picta* cranial morphology (Figure 0.5). Painted turtles possess a bicuspid tooth-like structure medial on the upper jawline that borders a "V"-shaped notch in the pre-maxillary bone (Figure 0.6, Figure 1.1). The pre-maxillary cusps are best termed tomiodonts, consistent with the description of these structures in Box Turtles, *Terrapene* sp. (Minx 1996; see Table A1.1). Records as early as 1993 in the Algonquin Painted Turtle database refer to some male *C*. *picta* possessing "fangs" or unusually long tomiodonts. Continued observational study of Algonquin Painted Turtles in 2010 and 2011 suggested that males had tomiodonts of more variable morphology (Figure 0.6) and often greater prominence than those of females. The putatively sexually dimorphic nature of the tomiodonts raised a number of questions about their morphology and possible adaptive significance.

The objective of the research in Chapter I is to assess whether cranial morphology, and tomiodont morphology in particular, is sexually dimorphic in *Chrysemys picta*. To address these ideas, sexual dimorphism in cranial structures was assessed in two ways: 1) the measurement and comparative analysis of established sexually dimorphic traits, putatively sexually dimorphic traits, and putatively non-sexual traits; 2) a visual survey whereby participants of varying experience levels were asked to classify lateral head photos of female and male *C. picta* based on specified cranial landmarks. If (sexually) selective factors are acting on the cranial morphology of *C. picta* then I predicted a sexual size and shape dimorphism of the tomiodonts and associated cranial morphology. Similarly, if tomiodonts are sexually dimorphic, then their morphology, including length, are expected to display high phenotypic variance and positive allometry in *C. picta*.

Methods

Study populations and sites

For morphometric analysis, *C. picta* were sampled from numerous study sites in Algonquin Provincial Park, Ontario, including the Arowhon population, Bat Lake, Broadwing Lake, Davies' Bog, Lake of Two Rivers, Madawaska River, Mew Lake, Oxtongue River, and Whitefish Lake. The Arowhon study population of *C. picta* is located at Wolf Howl Pond, Wolf Howl Pond East, and West Rose Lake (45°34'N, 78°41'W), where monitoring of population demographics and reproduction has taken place annually since 1978 (R.J. Brooks). A complete Arowhon site description can be found in Schwarzkopf and Brooks (1985). Algonquin Park *C. picta* are sympatric with

Snapping Turtles (*Chelydra serpentina*), and rarely, Blanding's Turtles (*Emydoidea blandingii*). Painted Turtles were captured by canoe or baited hoop trap and were subsequently transported and processed in the field lab at the Algonquin Wildlife Research Station (AWRS, Algonquin Provincial Park, Ontario, Canada).

Body and cranial morphometric traits

Consistent with the long-term study, injuries and abnormalities were recorded and eight body morphometric traits were measured using Vernier calipers (to the closest 0.01 cm), as follows: minimum and maximum carapace length, minimum and maximum plastron length, foreclaw length (left third phalange), maximum carapace width, maximum carapace height, and mass (g). Five additional cranial morphometric traits were measured with digital calipers (to the closest 0.001 cm) in mature females, mature males and juveniles: head length, head width, head depth, rostrum length, and jaw length (each defined in Table 1.1, Figure 1.8). Pre-cloacal tail length and hindclaw length (left third phalange) were measured (Table 1.1). When the left third foreclaw or left third hindclaw were absent or damaged, the right third foreclaw or right third hindclaw was measured instead. Due to the small size of tomiodonts (up to 3 mm) it was not feasible to measure these with digital calipers. Instead, high quality macro digital photographs were taken of the right lateral head (see *Visual survey of cranial morphology*) and frontal head using a Canon Rebel XTi digital SLR camera equipped with an 18-55 mm zoom lens. A 6 mm x 6 mm-grid was placed as a reference scale in each photograph. The head of each Painted Turtle was photographed in the same visual plane as the reference grid to ensure accurate scaling for future digital measurement. Tomiodont measurements were taken

from the frontal head photographs of *C. picta*. Photographs were imported into ImageJ software (Rasband 2014), scaled according to the reference grid and measured for left tomiodont length (mm), right tomiodont length (mm), tomiodont gap width (mm) (Table 1.1). A summary parameter, tomiodont length, was calculated from these three measurements using of the Law of Cosines (Appendix II). Finally, tomiodont splay angle was calculated (Table 1.1 and Appendix II).

Traits were grouped as putatively non-sexual (control variables), putatively sexual (test variables), and sexually dimorphic (positive controls) (Table 1.2). The unbiased selection of traits and comparisons of the allometric slopes between sexual and non-sexual traits provides a thorough test for an association between sexual selection and allometry (Bonduriansky 2007). That is, putatively non-sexual head measurements (Table 1.2) were chosen for comparison with known sexual traits and the putatively sexual traits (as per Tasikas *et al*. 2009; see *Statistical methods*). Morphometric traits were compared between the sexes to test for dimorphism. Potentially morphometric traits classed as putatively non-sexual may instead have been dimorphic, as was revealed by later analysis.

Each cranial morphometric trait (collected in 2012 and 2013), pre-cloacal tail length (collected 2013), and hindclaw length (collected 2013) were measured twice by two independent observers. For statistical analysis, the mean and coefficient of variation were calculated from the four measurements. Every trait could not be measured for every turtle resulting in unequal sample sizes among traits. Where measurements were collected in different years, the average metric between the two years was used in the subsequent analysis.

Qualitative evaluation of head dimorphism

A visual survey was conducted to qualitatively evaluate head shape sexual dimorphism in *C. picta*. The methodology and results of this survey are reported in Appendix III and Appendix IV.

Statistical analyses

Assessing allometry and phenotypic variation: Reduced major axis (RMA) regression was used to assess allometry in body and cranial morphometric traits. Reduced major axis assumes error in both the *x* and *y* variables (LaBarbera 1989, Warton *et al*. 2006, Claude 2008) making it well-suited because all morphometric traits were measured with potential error. Allometric slopes were constructed for all body and cranial traits in mature females, mature males and juveniles (unknown sex). All measurements were $\log_{10}$-transformed and regressed against $\log_{10}$-transformed midline plastron length as the standard body size metric. Midline plastron length was selected as the body size metric because this trait experiences the least amount of measurement error (unpublished data, Algonquin Provincial Park Painted Turtle database) compared to other body measurements (*e.g*., maximum plastron length, midline carapace length, maximum carapace length). Whereas I have used midplastron length as the preferred body size metric, it is recognized that other authors have recommended a linear measurement of carapace length as the body metric when examining sexual dimorphism (see Lovich *et al*. 1990*a*, Gibbons and Lovich 1990, Rowe 1997). Each allometric slope was tested for isometry (*i.e*., slope=1). Reduced major axis slope values significantly greater than 1

(positive allometry) are suggestive of sexually selected traits (Kodric-Brown *et al*. 2006; although not definitely attributable to sexual selection alone, see Bonduriansky 2007). Conducting a $\log_{10}$-transformation linearizes the relationship between the morphometric variables and meets the assumptions of normally distributed observations and residuals of equal variance (homoscedasticity). The assumption of homoscedasticity was not met for the juvenile traits head width, pre-cloacal tail length and hindclaw length, likely on account of small sample sizes. Pairwise male and female comparisons of allometric slopes for each trait were conducted to test for a common slope between the sexes (*e.g*. allometric slope of $\log_{10}$-tomiondont length plotted against $\log_{10}$-midline plastron length compared between males and females; Warton and Weber 2002).

The corrected coefficient of variation (CV') allows for a direct comparison of trait variation between established sexual traits and putatively sexual or non-sexual traits. To evaluate dispersion of datapoints around the RMA best fit regression line, the CV' was calculated for each putatively non-sexual, putatively sexual, and known sexual trait. The CV' accounts for variation in *y* when *x* is held constant and is suitable for evaluating variation in allometric slopes for sexual and non-sexual traits (Eberhard *et al*. 1998; also see Tasikas *et al*. 2009 and Schulte-Hostedde *et al*. 2011*a*). Generally, low phenotypic variance and isometry or negative allometry are expected from putatively non-sexual traits if they are truly non-sexual.

A Welch's t-test for unequal sample size and unequal variance was conducted on all size-adjusted traits to evaluate a difference in mean trait values between males and females. Reduced major axis analysis used Standardized Major Axis Tests and Routines (smatr) package, version 3, for *R* Statistical software (R Development Core Team 2013)

developed by Warton *et al*. (2012). Sample sizes (*n*) varied within groups and statistical tests because not every trait measurement was available for every individual.

Evaluation of defining cranial traits: The cranial traits of mature males and females were also analyzed using Linear Discriminant Analysis (LDA) with jackknife ("leave-one-out") cross validation to address two primary objectives: 1) how accurately can the sexes be grouped or distinguished according to cranial traits, and 2) which character(s) best predict group assignment (*i.e*., best separation between the sexes) by best representing phenotypic variation. Linear discriminant analysis is a descriptive multivariate statistical method that creates linear combinations (discriminant functions) of the variables to maximize the (sums of squares) difference between groups (in this case, the sexes) (Burns and Burns 2008, Claude 2008). The number of discriminant functions is equal to the number of groups-1. Therefore, a single discriminant function results from a LDA of two groups (sex; female and male), as is the case here. Coefficients of linear discriminants were computed to evaluate the contribution of each cranial trait in discriminant function 1. A follow-up predictive model was applied to linear discriminant 1 to assess its predictive performance in correctly identifying the sex of an individual when group membership (*i.e*., sex) was masked. Jackknife cross validation is considered to be a more honest representation of discriminant function performance because it avoids self-influence from the original dataset in the predictive model (Burns and Burns 2008). A post-hoc Wilks' Lambda Test was conducted to confirm which variable(s) contributes significantly to the discriminant function and which cranial characters differed between the sexes. The LDA was completed in R statistical software (R

Development Core Team 2013) using the MASS package (Venables and Ripley 2002). All head traits were standardized against midline plastron length prior to analysis. The LDA was limited to turtles of known sex with a complete set of cranial trait measurements (n=145; n_{female}=75, n_{male}=70).

Results

Sexual dimorphism in body and cranial morphometric traits

Among female and male Painted Turtles, 13 traits (2 putatively non-sexual, 7 putatively sexual, and 4 sexually dimorphic traits; Table 1.2) were measured and assessed for dimorphism. Taken together, head morphometric traits were significantly different between females and males (Wilks' $\lambda = 0.5127$, $F_{6,133} = 21.067$, $p < 0.001$; Table 1.3). Male *C. picta* were significantly larger than females in relative head length ($t_{280} = 9.47$, $p < 0.001$), head width ($t_{280} = 6.28$, $p < 0.001$), head depth ($t_{280} = 6.82$, $p < 0.001$), rostrum length ($t_{253} = 113.25$, $p < 0.001$), jaw length ($t_{184} = 2.31$, $p < 0.05$), tomiodont gap width ($t_{143} = 3.76$, $p < 0.001$), tomiodont length ($t_{118} = 9.29$, $p < 0.001$), carapace length ($t_{269} = 9.48$, $p < 0.001$), and carapace width ($t_{282} = 6.16$, $p < 0.001$) (Table 1.3). Among known sexual traits, size-adjusted foreclaw length ($t_{251} = 26.66$, $p < 0.001$) and pre-cloacal tail length ($t_{176} = 24.90$, $p < 0.001$) were significantly greater in males, whereas carapace height was significantly greater in females ($t_{279} = 7.74$, $p < 0.001$). Hindclaw length, a putatively non-sexual trait, did not differ between the sexes ($t_{143} = 0.21$, $p > 0.05$). Lastly, females had a significantly larger mean tomiodont splay angle than males ($t_{142} = 2.09$, $p < 0.05$).

Allometry of body and cranial morphometric traits

All correlations between body or cranial traits and midline plastron length of females and males were highly significant ($p<0.001$ in all cases). For juveniles, most correlations between the morphometric traits and body size were significant ($p < 0.05$), excluding pre-cloacal tail length ($p = 0.14$) and tomiodont gap width ($p = 0.059$).

The RMA slope values of all traits, excluding tomiodont length and tomiodont gap width, regressed against midline plastron length differed significantly between females and males (Table 1.4). Despite very similar slope values (DF = 1, $p = 0.96$, as per Warton and Weber 2002), the elevation (*i.e.*, y-intercept) of tomiodont length differed significantly between the sexes (Wald statistic = 144.3, DF = 1, $p < 0.001$; Figure 1.2*a*). The elevation of tomiodont gap width RMA line of best fit was also significantly different between females and males (Wald statistic = 43.82, DF = 1, $p < 0.001$, Figure 1.2*b*). Both females and males displayed strong positive allometric slopes for tomiodont measurements (Table 1.4). The tomiodonts of mature males were proportionately larger than those of females across all body sizes (Figure 1.2*a*).

Overall, the fitted RMA regression line explained most of the variation for shell size (carapace length, width and height) and some cranial traits (head length, width depth, and rostral length) (Table 1.4). A positive and linear, albeit weak, relationship was detected between tomiodont length and body size in females (RMA, $n = 74$, $R^2 = 0.014$, $p < 0.001$). Male tomiodont length increased with body size (RMA, $n = 72$, $R^2 = 0.42$, $p < 0.001$). Despite a small sample size, a positive, linear and comparatively strong correlation was found between tomiodont length and body size in juveniles (RMA, $n = 5$,

$R^2 = 0.81$, $p < 0.05$). The RMA plots indicate that both females and males demonstrate high phenotypic variation in tomiodont morphology (Figure 1.2).

Positive allometric slopes were common among cranial traits for males (5 of 7 metrics, 71%), but comparatively low for females (2 of 7 metrics, 29%) (Table 1.4). Juveniles did not exhibit positive allometry for any cranial or body traits (Table 1.5). Among all 13 body and cranial traits, 4 traits exhibited isometry, 5 traits negative allometry, and 4 traits positive allometry in females. Among all 13 body and cranial traits in males, 3 traits reflected isometry, 1 trait negative allometry and 9 traits positive allometry. Lastly, juveniles demonstrated isometry in 7 traits and negative allometry in the remaining 6 traits among all 13 traits (Table 1.5).

Variation in body and cranial morphometric traits

For known male sexual traits (*e.g.*, pre-cloacal tail length and foreclaw length) the CV' values are among the largest measured (Table 1.3). In addition, the CV' values for the putatively sexual traits tomiodont length and tomiodont gap width are very large for adults of both sexes and the CV' for male rostrum length is notably large (Table 1.3). The known female sexual traits, such as greater carapace length and height, have a mid-range CV' values similar to putatively non-sexual traits. Putatively sexual traits in females, including smaller jaw length and head length, width, and depth have relatively low CV' values similar to putatively non-sexual traits.

Positively allometric RMA slopes were coincident with high CV' values for morphological traits in *C. picta*, particularly for male sexual traits foreclaw length, pre-

cloacal tail length, and putatively sexual rostrum length, tomiodont length and tomiodont gap width.

Defining cranial traits and sex-specific classification

In linear discriminant 1, the greatest loadings were assigned to tomiodont length (LDA coefficient = 284.15), followed by rostrum length (74.23) and jaw length (66.63). Head length (46.55), head depth (9.86), and head width (-23.54) contributed relatively little to the distinction between the sexes. Linear discriminant 1 did not achieve full separation of males and females based on cranial traits. A stacked histogram of linear discriminant 1 values for cranial measures of males and females demonstrate overlap between the sexes at values of -1 to 1 (Figure 1.3). Males cluster at the high end of discriminant function values (values 1 to 4) whereas females cluster low (values -3 to 1). In testing the predictive LDA model, males and females could be distinguished with 88.57% accuracy (misclassification rate of 11.43%) based on cranial traits. Females were 12.31% likely to be misclassified as male and males were 13.56% likely to be misclassified as females. Jackknife ("leave one out") cross validation resulted in an increased overall misclassification rate to 14.29%. The misclassification rate of females rose marginally to 14.52% and the misclassification of males increased to 18.97%.

Discussion

Summary of findings

A total of 13 body and cranial morphometric traits were tested for allometry and sexual dimorphism in mature female and male *C. p. marginata* of Algonquin Provincial

Park. Male rostrum length, jaw length, tomiodont length, tomiodont gap width and head depth demonstrated positive allometry and high levels of phenotypic variation, consistent with the expectation for sexual traits. The tomiodonts of females also grew with positive allometry, although in proportion to body size males have larger tomiodonts than those of females. The largest males had the largest mean tomiodont lengths (Figure 1.2*a*). In addition, males consistently had larger head proportions, including a longer rostrum, head width and jaw length. Foreclaw length, a sexual trait, grows isometrically in mature males. This suggests that following the drastic foreclaw elongation at time of maturity, males continue to maintain the trait but do not invest heavily in it. The putatively non-sexual traits, carapace width and hindclaw length, were fairly poor control variables because of their inconsistent patterns of allometry and phenotypic variation. Carapace width was negatively allometric in both sexes, as opposed to expectations of isometry. In addition, hindclaw length exhibited high phenotypic variation and positive allometry in males.

In juveniles, most cranial and body traits scaled in isometry, although these results are to be interpreted with caution because of a small sample. Regardless, there is biological justification for this outcome. Considering that the mean size of juveniles sampled (91.25 mm midline plastron length) approximates the lower size bound at which secondary sexual traits begin to manifest in the Arowhon population (~90 mm plastron length, Samson 2003), secondary sexual traits, and thereby outcomes of positive allometry, are not likely. The high number of negative allometric slopes for juvenile cranial traits, such as head length and width, rostrum length and jaw length, are also consistent with expectation. Young turtles have disproportionately large heads that scale

negatively with body size throughout ontogeny (Herrel and O'Reilly 2006, Bever 2008, 2009), as is the case with young of many animals (Gould 1966, Emerson and Bramble 1993). Most dimensions of the skull scale with negative allometry during postnatal growth (Bever 2009), unless associated with the feeding apparatus (*e.g.*, triturating surface of the *Pseudemys* jaw; Bever 2008), ornamentation, or weaponry (*e.g.*, horns; Kazuo 1995). A visual comparison of juvenile *C. picta* with adult females (Figure 1.4) and adult males (Figure 1.5) of different body sizes provides a perspective of the ontogeny, and perhaps heterchrony, of cranial dimorphism. Males exhibiting the extreme dimorphic phenotype are also shown for comparative purposes (Figure 1.6).

What mechanisms or processes are responsible for the observed dimorphism?

Cranial differences between female and male *C. picta* have been shown statistically and visually (Appendix III), lending support to the hypothesis that cranial structure, including tomiodont morphology, is sexually dimorphic in this species (at least in my study population in Algonquin Provincial Park). But why would the cranial structure of females and males differ? Ecological and sexual selection hypotheses can be proposed to explain the observed dimorphism, but not without challenges. A conflict arises in trying to tease apart the mechanism underlying tomiodont dimorphism. Tomiodonts are outgrowths of the premaxillary bone and, therefore, are either directly or indirectly associated with feeding (given their position on the upper jawline). As field observations would suggest, the tomiodonts may also have a functional significance related to reproduction if males use their tomiodonts to bite and secure females during copulation (see Chapter III). Shine (1989, 1991) recognized that character divergence in

feeding structures can lend strong support for ecologically-based dimorphisms, but that such a test cannot be applied to most animal taxa because feeding structures may also be modified by sexual selection based on the reproductive roles of each sex. Thus, an ideal species or group in which to assess ecologically-based dimorphisms would require that feeding structures be independent of sexual interactions, such as courtship, mating, or combat (*e.g.*, Serpentes, Shine 1991). For a dimorphic feeding structure, an ecological mechanism can only be accurately inferred if the direction of the trait is opposite that expected by sexual selection (Shine 1991). In the case of tomiodonts, an ecological (dietary) and a sexual selection mechanism both point in the same direction of dimorphism: positive allometry, or elongation of the tomiodonts. That is, positive tomiodont allometry may be a result of ecological and/or sexual selection.

Below, I systematically address each of the ecological and sexual mechanisms that may be acting on tomiodont morphology. I will argue that there is stronger evidence for sexual selection than an ecologically-based mechanism.

Dietary partitioning as an ecological mechanism for tomiodont dimorphism

Tomiodont dimorphism may be attributed to an ecological mechanism in two different ways. Firstly, the tomiodonts may assist directly in feeding. If the tomiodonts of *C. picta* are a trophic adaptation, then we would expect that the trait is related to food acquisition and any observed dimorphism reflects inter-sexual diet specialization. Dietary niche divergence is reported in turtle species and is coupled with sex-specific adaptations of the feeding apparatus. For instance, the wide head, hypertrophic jaw muscles and broad alveolar surface of female Map Turtles (*Graptemys* sp.) permits the exploitation of

mollusks not accessible to males (Lindeman 2000, Bulté *et al*. 2008). Further, the larger jaw and greater jaw adductor muscle mass of female Diamond-back Terrapins (*Malaclemys terrapin*) increase bite force, reduce prey handling time, and allow differential resource use between the sexes, thereby reducing competition (Underwood *et al*. 2013). The dietary divergence hypothesis has also been tested in relation to cranial dimorphism in male lacertid lizards, which exhibit a larger head size and greater bite force compared to females (Herrel *et al*. 1996, 1999, Verwaijen *et al*. 2002, Huyghe *et al*. 2009). Evidence for an ecological (diet) mechanism related to the head dimorphism was found the lactertid lizard studies, although a non-mutually exclusive sexual selection hypothesis has also been proposed (see *Sexual mechanism* discussion below; Herrel *et al*. 1996, 1999, Huyghe *et al*. 2009)

Alternatively, dimorphism of a feeding apparatus (*e.g*., beak, jaws, teeth) can be indirectly related to reproduction via energy acquisition (Bulté *et al*. 2008). The hypothesis that reproductive roles predispose sexual dimorphism has been tested in diverse taxa, including spiders (Walker and Rypstra 2002), fish (Casselman and Schulte-Hostedde 2004, Cott *et al*. 2013), rodents (Schulte-Hostedde *et al*. 2001), turtles (Lindeman 2000, Bulté *et al*. 2008), and snakes (Shine 1991, Bonnet *et al*. 1998) (see Fairbairn *et al*. (2007) for taxonomic overview). Female-biased dimorphism is expected when a trait aids in energy procurement, since the acquisition of energy is critically important for female reproduction (Casselman and Schulte-Hostedde 2004, Herrel and O'Reilly 2006, Bulté *et al*. 2008). Thus, we might expect that positive selection would act on female head size (*e.g*., Bulté *et al*. 2008) or tomiodont morphology if an increase in the size of either of these structures would facilitate energy acquisition; however, I did

not observe a proportionately larger head and tomiodont size in female relative to male *C. picta*. Males too experience positive allometry in cranial traits and disproportionately large tomiodonts.

Ontogenetic changes in cranial structure, especially that of the jaw, can be associated with increased bite force and improved feeding performance. Hypertrophy of the skull, jaw musculature and triturating surfaces of the jaw are reported for turtle species that experience an ontogenetic dietary shift toward durophagy, the consumption of hard-shelled prey (Bulté *et al*. 2008, Pfaller *et al*. 2009). The well-developed jaw, long medial lower jaw hook, broad gape, and distinctive tricuspid tomiodont arrangement of the Narrow-bridged Musk Turtle (*Claudius angustatus*) likely reflect their dietary specialization on crustaceans (Legler and Vogt 2013). In the Leatherback Sea Turtle (*Dermochelys coriacea*), the deep premaxillary notch coupled with prominent bicuspid tomiodonts may be involved in handling soft-bodied prey (Prichard 1977). A serrated tomium is recorded in Cooters (*Pseudemys* sp.; Leary *et al*. 2008, Jackson 2010) and the Green Sea Turtle (*Chelonia mydas*; Balazs 1980) for shearing vegetation. The large Asian river turtle *Batagur baska* has a deep premaxillary notch and bicuspid tomiodonts that are reportedly used to cut tough plant materials (Davenport *et al*. 1992, Anderson and LaBarbera 2008) such as leaves, stems and *Sonneratia* mangrove fruits (Ernst *et al*. 2006, Moll *et al*. 2009). Could tomiodonts assist *C. picta* in feeding? Is an ecologically based mechanism, namely dietary partitioning, a viable explanation for the observed tomiodont sexual dimorphism in *C. picta*?

I found tomiodont isometry in juveniles, positive allometry in females, and positive allometry with a proportionately large tomiodont size in males. If the tomiodonts

are important in feeding they appear to be most important in adulthood and of particular importance for males. There are no known dietary or sex-specific feeding specializations in *Chrysemys* (Ernst and Lovich 2009, Padgett *et al*. 2010), thus modification of cranial morphology for dietary reasons seems unlikely and would be particularly curious in the case of males. Further, dietary partitioning (or rather, a lack thereof) does not explain why overall differences in cranial structure (rostrum length, jaw length, head width, *et cetera*) would exist between the sexes. Ecological selective forces from diet fail to account for why males have large tomiodonts when females should theoretically demonstrate the more extreme dimorphism owing to their reproductive demands (reproductive role hypothesis).

Alternative reproductive tactics as a sexual mechanism for tomiodont dimorphism

Rather than necessarily investing in a trait that will assist in energy gain, as is the case with females, males are expected to demonstrate dimorphism via enlarged or exaggerated traits that improve mate acquisition (Andersson 1994, Casselman and Schulte-Hostedde 2004, Bulté *et al*. 2008). Male-biased dimorphism and positive head allometry are recorded in lacertid lizards: males immobilize females during copulation via biting, and dimorphic jaw musculature and the resulting greater bite force of males is important to coerce females during courtship (Herrel *et al*. 1996, 1999, Huyghe *et al*. 2009, Ljubisavljević *et al*. 2008).

Painted turtles demonstrate a polygamous mating system (Wilbur and Morin 1988). Males may sire multiple clutches of eggs (at least in part) with multiple females in a single breeding season and females may lay mixed paternity clutches (Pearce and Avise

2001, Pearce *et al*. 2002, Uller and Olsson 2008, McGuire *et al*. 2011, McGuire *et al*. 2014). Female *C*. *picta* are also capable of long-term sperm storage and fertilize multiple clutches within and between years from sperm obtained during a single copulation (Uller and Olsson 2008, McGuire *et al*. 2011, McGuire *et al*. 2014). The repeated use of stored sperm to fertilize successive clutches within and among years can increase a male's reproductive success considerably (McGuire *et al*. 2011, McGuire *et al*. 2014). Males potentially have a lot to gain from even a single copulation. Thus, strong selective pressure would exist to develop mating tactics (*e*.*g*., coercion) and/or secondary sexual structures (*e*.*g*., tomiodonts) that maximize copulation success.

Why and how might tomiodonts be related to alternative (coercive) mating tactics in *C*. *picta*? I propose that males utilize the tomiodonts as sexual weapons to coerce females into mating. Berry and Shine (1980) suggest that forced insemination is an unreliable mating strategy in aquatic, free swimming turtles because of the large and open habitat they occupy, the high mobility of individuals and the ease with which females would be capable of escaping from males. Because *C*. *picta* females are larger than males, successful copulation is only likely if a female is receptive or immobilized. A bite using the tomiodonts may function as part of a pre-copulatory courtship involving immobilization of the female in order for a male to mount. Similarly, the tomiodonts with their bicuspid sharp points may serve to secure a grip on the soft tissue of the female's neck while a male is mounted. Extensive fresh and scarred wounds have been observed on the head and neck of females in the Arowhon *C*. *picta* population of Algonquin Provincial Park (Chapter II). Additionally, *in situ* field observations and experimental trials have recorded males acting agonistically with females, including chasing, biting of

the head and nape, aggressive ramming, and extended periods of forced submergence (Chapter III). If it is shown that wounding is more common on females compared to males and juveniles, then there would be additional evidence that females are the target of male aggressive interactions related to reproduction. If males adopt coercive mating tactics (an alternative to the traditionally recognized titillation-type courtship; Taylor 1933, Cagle 1954, Ernst 1971, Berry and Shine 1980, Ernst and Lovich 2009) involving biting and the immobilization females to achieve copulation, there would exist strong evidence that the tomiodont dimorphism has a sexual selection basis. Further discussion on the putative relationship between tomiodonts, coercive mating behaviours, mating success, and proximate and ultimate causation for these phenomena is presented in Chapter III.

Of course, females also exhibit positive allometry in tomiodont length and gap width. Why might females exhibit positive allometry in tomiodont characters if these structures are not being used for feeding or mating? A small number of observations exist within the Arowhon population of females directing aggressive behaviours toward conspecifics. Perhaps the tomiodonts of females also serve as defensive structures and thereby maintain positive allometry through a mechanism independent of feeding or sexual selection. For instance, female Smooth Softshell Turtles (*Apalone mutica*) that are unreceptive to a male's advances aggressively charge and bite males to prevent copulation (Plummer 1977). Also, genetic correlation between the sexes may explain morphometric similarities. As Minx (1996) noted with Box Turtles (*Terrapene*), older individuals had bicuspid tomiondonts that were obscured or absent due to wear. Likewise, tomiodont wearing has been observed in the Alabama Red-bellied Cooter,

Pseudemys alabamensis (Leary *et al*. 2008, D. Nelson, pers. comm. 2014). Although the origin and structure of tomiodonts remain unknown, these structures appear to be composed of premaxillary bone overlain by keratin (pers. obs., see Figure 0.7). Perhaps the positive allometry observed in females is an artefact of compensatory or maintenance growth of the upper beak following regular wear. That is, the tomiodonts of females may experience steady growth that offsets wear. Wild Painted Turtles are capable of reaching at least 60 years of age (Congdon *et al*. 2003) and individuals of at least 50 years are known in the Arowhon population (R. Brooks, unpublished data, pers. comm.). Whether there are differential wear patterns between females and males remains to be addressed.

Lastly, what would account for the contrasting overall head morphology between the female and male *C*. *picta* of Algonquin Provincial Park? As noted previously for Mesoamerican *Trachemys* (see General Introduction), the elongation of the snout and distinctive cranial profile of males may serve in mate recognition or an "erotic prod" for females (Legler 1990, Legler and Vogt 2013). With respect to the ecological (diet) hypothesis, there is no obvious relationship between sex-specific variation in snout shape and diet as *C*. *picta* are generalist feeders (Ernst and Lovich 2009, Padgett *et al*. 2010).

The functional significance of tomiodont morphology

Dental structures are critically important for feeding and serve numerous purposes, including prey incapacitation, food handling, fragmentation and ingestion. Chelonians do not have teeth but rather a keratinized beak that may be highly modified, displaying a range of alveolar (crushing surfaces) and tomium (cutting surfaces) configurations. Likewise, the anterior beak morphology of chelonians is highly variable,

from a well-rounded and deep premaxillary notch (e.g., *Emydoidea blandingii*), to a single sharp apical tomiodont (*e.g.*, *Chelydra serpentina*, *Macrochelys temminckii*), bicuspid, or relatively rare tricuspid arrangement (*e.g.*, *Claudius angustatus*, *Indotestudo elongata*). Bicuspid tomiodonts are observed in a number of distantly related species (Appendix I, Table A1.2).

Experimental studies have examined the functional consequences of tooth design with respect to performance. Notched blades perform best in the capture and restraint of tough, malleable materials (prey or the soft tissue of conspecifics or predators) and permit fracture with minimal deformation (Lucas 2004, Anderson and LaBarbera 2008). The tomiodont structure of *C. picta* closely parallels a triangle and notch tooth description (*i.e.*, a high performance design). The combination of triangular blades and an acute notch generate the greatest bite force with the least amount of work and reduce the level of strain exerted on the bite object (Anderson and LaBarbera 2008). The mean tomiodont splay angle is significantly reduced ($p < 0.05$) in males (69.92°) compared to females (72.84°), which may confer differential tomiodont performance between the sexes. From a biological (biomechanical) standpoint, the improved cutting and gripping performance indicative of male *C. picta* tomiodont morphology has numerous implications. Consistent with the findings of Anderson and LaBarbera (2008), I propose that male *C. picta* are capable of higher bite force generation at the site of the tomiodonts and more effective and efficient grasping capabilities on account of a longer tomiodont (blade) length and shallower notch angle. Bite force may be further modified in the sexes due to other differences in cranial morphology (*i.e.*, jaw length, jaw muscle mass, cranial shape and size; Herrel *et al*. (1996), Ljubisavljević *et al*. (2008), Huyghe *et al*. (2009)). These

features may be related to male performance during coercive mating (Chapter III). Differences in cranial morphology (size and shape) betweent the sexes may be attributable to skeletal anatomy, muscular anatomy, or both.

Size at maturity and post-maturity tomiodont growth

Adult male and female *C. picta* differ in the intercept but not in the slope of the tomiodont length-body size allometry. Thus, males have proportionally larger tomiodonts than females across all body sizes despite very similar post-maturity growth rates of the tomiodonts (RMA slope values, Table 1.4). This would indicate that males have an earlier onset of tomiodont growth. In the Arowhon population, male *C. picta* mature at approximately 90 mm plastron length, whereas females mature at approximately 120 mm (Samson 2003). If tomiodont growth (lengthening) occurs at maturity, males would experience an earlier onset of positively allometric tomiodont growth than females. This would explain why males maintain proportionately larger tomiodonts across all post-maturity body sizes. Rather than investing in a large adult body size and high reproductive costs at maturity (as is the case for females; see discussion of the reproductive roles hypothesis above), instead males begin to allocate their energy resources to secondary sexual structures that would enhance mating opportunities; first the foreclaws (titillation courtship) and perhaps later the tomiodonts (coercive courtship).

A novel putative carapace dimorphism in C. picta

Over the course of sampling from 2010-2013, a putative sexual dimorphism of the carapace was noted. Larger (and potentially older) male *C. picta* appear to develop a

projecting nuchal bone that extends beyond the anterior edge of the carapace (Figure 1.7*d*). In addition, the first left and first right anterior marginal scutes of larger males tend to flare away from the cervical scute leaving deep natural notches on either side of the cervical giving it the appearance of a battering ram. The cervical scute and the adjacent marginal scutes may also be serrated and sharp, and often co-occur with large tomiodonts, forming a suite (arsenal) of sexually dimorphic weapons. These traits are in contrast to most females for whom the cervical scute is flush with the adjacent scutes forming a continuous edge along the anterior carapace. Remarks from the Algonquin Painted Turtle database first make mention of these traits in 1995, with observations steadily increasing thereafter. Reports from the literature have been compiled (Appendix I, Table A1.3) and show that these traits have been mentioned across *Chrysemys* subspecies, but there is no mention of sexual dimorphism of these traits in the literature. The projecting cervical scute and serrated marginal sutes are reminiscent of the projecting gular scutes of tortoises, described in the context of combat and mating (see *Sexual dimorphism in chelonians* in General Introduction).

A male Painted Turtle (ID 1893 notch) from the Algonquin Park Arowhon population is of particular interest with respect to tomiodont and carapace morphology. This relatively large male (13.47 mm midline plastron length and 14.89 midline carapace length in 2013) has been in the study since 1984 and best epitomizes an extreme example of tomiodont structure (Figure 1.7). In lateral profile this turtle has a long snout, flat rostral-orbital distance, and large tomiodonts that overhang the lower jaw (Figure 1.7*a*). In fact, male ID 1983 notch has a tomiodont length of 2.41mm, the largest measured to date. Uniquely, the tomium of the upper beak is also highly serrated on both the left and

right, immediately posterior to the tomiodonts (Figure 1.7*b*,*c*). This male also demonstrates deep natural notches on either side of the cervical scute (nuchal bone), coupled with serrations on the cervical and adjacent anterior marginal scutes (Figure 1.7*d*). Observations of male *C. picta* with the abovementioned modifications to the anterior carapace are not restricted to our sites in Algonquin Provincial Park, also having been anecdotally described from: Sudbury District, Ontario (D.L. LeGros and C.L. Comeau, Figure 1.7*e*); numerous sampled populations throughout Ontario (S. Carstairs, Ontario Turtle Conservation Centre, pers. comm. 2014); Beaver Island, Michigan (J. Rowe, pers comm. 2014); and numerous sampled populations throughout Georgia (S. Sterret, pers. comm. 2014).

Future directions and conclusions

Sexual dimorphism in the head structure of *C. picta* raises many questions about the underlying mechanism(s) generating these differences and how these mechanisms and traits interact with the organism's ecology and evolution. Future workers should investigate the relationship between chelonian beak morphology, phylogeny, diet and reproductive strategy. A character matrix displaying species, tomiodont structure (notched, mono-cusp, bicuspid, tricuspid) and aspects of the species' biology may help to elucidate patterns of beak morphology. The osteology, ontology and heterochrony of the tomiodonts and head structure of *C. picta* are important for a better understanding of the development of these structures. Although I have examined tomiodont morphology in relation to size, future research should also target the relationship between tomiodont morphology and age. Biomechanical assessments, such as bite force, should be conducted

with female and male *C. picta* to measure performance and better evaluate the functional significance of head dimorphism.

Following nearly 180 years of simple descriptive reference to the tomiodonts in *C. picta*, my study is the first quantitative investigation of the subject. The findings presented here demonstrate clear morphological differentiation and divergence between the sexes of *C. picta* with respect to head morphology. Chapter I demonstrated that the head morphology of *C. picta* from Algonquin Provincial Park is sexually dimorphic. These findings describe the form of the tomiodonts, among other cranial traits, and provide the framework upon which the rest of this thesis is built. Chapters II and III address the function of the tomiodonts and test their functional significance as part of alternative coercive reproductive tactics in *C. picta*.

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Table 1.1: Body and cranial traits measured in mature male and female and in juvenile Painted Turtles (*Chrysemys picta marginata*) of Algonquin Provincial Park. Also see Figure 1.1 for visual representation of cranial morphometric traits.

Trait	Definition
Body morphometric traits	
Midline carapace length (MidCL)	Straight line measurement extending from centre of cervical scute (nuchal bone) at anterior to between the twelfth left and twelfth right marginal at posterior
Midline plastron length (MidPL)	Straight line measurement extending from between the gular (first plastral) scutes at anterior to between the anal (sixth plastral) scutes at posterior
Foreclaw length (LF3)	Left front third phalange
Carapace width (CW)	Straight line measurement across carapace at widest point
Carapace height (CH)	Maximum shell height
Hindclaw length (LH3)	Left hind third phalange
Pre-cloacal tail length	Length from posterior-most point of plastron to posterior-most edge of cloaca opening
Cranial morphometric traits	
Head length (HL)	Anterior-most rostrum to posterior edge of tympanum
Head width (HW)	Widest point across mid-tympanum
Head depth (HD)	Dorsal rostrum to ventral lower mandible with mouth completely closed
Rostral length (RL)	Pre-orbital, anterior-most rostrum to front of eye socket
Mandible length (ML)	Upper jaw sheath length, anterior to posterior length of upper jaw
Tomiodont length	Summary measurement derived from Cosine law, involving left tomiodont length, right tomiodont length and tomiodont gap width Left tomiodont length: measurement extending from the centre of the premaxillary notch to the distal tip of the left tomiodont Right tomiodont length: measurement extending from the centre of the premaxillary notch to the distal tip of the right tomiodont
Tomiodont gap width	Distance between the tip of the left and tip of the right tomiodont. If the left and right tomiodont were of different lengths this measurement would be diagonal
Tomiodont splay angle	Acute angle of premaxillary notch between the base of the tomiodonts. Measured in degrees (°).

Table 1.2: Grouping of body and cranial morphometric traits according to their categorization as being putatively non-sexual, putatively sexual, or sexually dimorphic measured in mature female (F), mature male (M), and juvenile Painted Turtles (*Chrysemys picta marginata*) of Algonquin Provincial Park. Definitions for each trait can be found in Table 1.1.

Putatively non-sexual (control variables)	**Putatively sexual** (test variables)	**Sexually dimorphic** (positive control variables)
Carapace width	Head length	Carapace length (F > M)
Hindclaw length	Head width	Carapace height (F > M)
	Head depth	Foreclaw length (F < M)
	Rostrum length	Pre-cloacal tail length (F < M)
	Mandible length	
	Tomiodont length	
	Tomiodont gap width	

Table 1.3: Descriptive statistics of body and cranial morphometric traits in Midland Painted Turtles (*Chrysemys picta marginata*) of Algonquin Provincial Park. Sample size (*n*) is representative of raw measurements. The mean of the raw measurements ($\bar{x}$) and mean of size-adjusted measurements ($\bar{x}$') are presented. The corrected coefficient of variation (CV', expressed as %) was calculated for untransformed data. Tomiodont splay angle was not standardized against midline plastron length.

	Female					**Male**				
	n	$\bar{x}$	$\bar{x}$'	**SD**	**CV'**	***n***	$\bar{x}$	$\bar{x}$'	**SD**	**CV'**
Putatively non-sexual traits										
Carapace width	138	115.01	0.81	10.22	2.81	147	103.90	0.83	9.34	3.09
Hindclaw	93	9.74	0.068	0.95	8.13	99	8.58	0.068	1.30	6.56
Putatively sexual traits										
Head length	137	26.00	0.18	2.12	3.11	147	24.02	0.19	2.40	3.94
Head width	138	22.75	0.16	1.86	3.52	145	20.82	0.17	2.14	4.58
Head depth	138	13.22	0.093	1.29	5.19	146	12.18	0.097	1.30	5.17
Rostral length	137	5.79	0.041	0.54	4.91	146	5.69	0.046	0.69	11.50
Jaw length	137	13.33	0.094	1.21	4.82	142	12.28	0.097	1.29	7.15
Tomiodont length	74	0.90	$6.2e^{-3}$	0.24	26.34	72	1.24	$9.7e^{-3}$	0.40	24.74
Tomiodont gap width	75	1.23	$8.5e^{-3}$	0.23	18.27	72	1.21	$9.5e^{-3}$	0.27	17.81
Sexual traits										
Carapace length	138	150.96	1.065	14.65	1.67	147	136.31	1.091	14.4	2.23
Carapace height	137	54.30	0.38	5.35	4.45	147	45.70	0.37	4.31	8.78
Foreclaw	134	7.45	0.052	1.00	11.68	143	11.43	0.092	1.68	14.09
Pre-cloacal tail length	93	12.91	0.090	3.09	21.08	98	21.70	0.17	3.69	14.73
Miscellaneous trait										
Tomiodont splay angle (°)	74	73.84	*NA*	14.48	*NA*	70	69.62	*NA*	8.95	*NA*

Table 1.4: Summary statistics of Reduced Major Axis (RMA) regressions of cranial and body morphometric traits for mature female and male *Chrysemys picta* of Algonquin Provincial Park (Ontario, Canada). Number of samples in RMAs presented following each trait name (female:male). Coefficient of determination (R^2), RMA slope, and 95% confidence intervals (95% CI) reported from RMA analysis. Superscript $^{(+)}$ represents significantly positive allometric trait, superscript $^{(-)}$ represents significant negative allometric trait (slope significantly different from 1) for RMA slopes. Likelihood ratio (LR) and *p*-value ($\alpha = 0.05$) presented for test of common RMA slope between females and males (degrees of freedom = 1 in all tests of common RMA slope).

	Female			Male				
	R^2	**RMA slope**	**95% CI**	**R^2**	**RMA slope**	**95% CI**	**LR**	***p***
Putatively non-sexual traits								
Carapace width (138:147)	0.90	0.88^{-}	0.83-0.92	0.88	0.91^{-}	0.86-0.97	1.10	> 0.05
Hindclaw length (93:99)	0.30	1.06	0.88-1.26	0.14	1.39^{+}	1.16-1.68	4.45	< 0.05
Putatively sexual traits								
Head length (137:147)	0.85	0.80^{-}	0.75-0.85	0.85	1.03	0.97-1.10	28.22	< 0.001
Head width (137:145)	0.82	0.80^{-}	0.74-0.86	0.80	1.04	0.96-1.12	24.65	< 0.001
Head depth (138:146)	0.72	0.94	0.86-1.02	0.77	1.09^{+}	1.00-1.18	6.06	< 0.05
Rostral length (136:146)	0.73	0.92	0.84-1.01	0.66	1.22^{+}	1.11-1.35	17.73	< 0.001
Jaw length (137:142)	0.72	0.90^{-}	0.82-0.98	0.54	1.22^{+}	1.09-1.36	16.79	< 0.001
Tomiodont length (74:72)	0.014	3.41^{+}	2.70-4.29	0.42	3.38^{+}	2.82-4.05	2.62×10^{-3}	> 0.05
Tomiodont gap width (75:72)	0.034	2.31^{+}	1.84-2.89	0.35	2.11^{+}	1.74-2.56	0.35	> 0.05
Sexual traits								
Carapace length (138:147)	0.97	0.97^{-}	0.94-1.00	0.96	1.09^{+}	1.06-1.13	26.64	< 0.001
Carapace height (137:147)	0.80	0.97	0.90-1.05	0.13	2.06^{+}	1.77-2.40	70.64	< 0.001
Foreclaw length (137:146)	0.24	1.40^{+}	1.21-1.63	0.075	1.09	0.93-1.28	5.10	< 0.05
Pre-cloacal tail length (93:98)	0.22	2.67^{+}	2.22-3.20	0.25	1.94^{+}	1.63-2.31	6.10	< 0.05

Table 1.5: Summary statistics of Reduced Major Axis regressions of cranial and body morphometric trait for juvenile *Chrysemys picta* of Algonquin Provincial Park (Ontario, Canada). Number of samples in RMAs presented following each morphometric trait name. Coefficient of determination (R^2), RMA slope, and 95% confidence intervals (95% CI) reported from RMA analysis. Superscript $^{(+)}$ represents significantly positive allometric trait, superscript $^{(-)}$ represents significant negative allometric trait (slope significantly different from 1) for RMA slopes. Likelihood ratio (LR) and *p*-value ($\alpha = 0.05$) presented for test of common RMA slope between females and males (degrees of freedom = 1 in all tests of common RMA slope).

	Juvenile						
	R^2	**RMA slope**	**95% CI**	**$\bar{x}$**	**$\bar{x}$'**	**SD**	**CV'**
Putatively non-sexual traits							
Carapace width (9)	0.99	0.70^{-}	0.65-0.75	81.38	0.90	10.54	0.013
Hindclaw length (5)	0.93	0.94	0.58-1.51	6.20	0.071	1.31	0.056
Putatively sexual traits							
Head length (9)	0.96	0.68^{-}	0.57-0.81	18.90	0.21	2.38	0.13
Head width (9)	0.74	0.80	0.51-1.24	16.52	0.18	2.46	0.076
Head depth (9)	0.96	0.74^{-}	0.62-0.88	9.72	0.11	1.33	0.027
Rostral length (9)	0.87	0.61^{-}	0.45-0.84	4.26	0.048	0.50	0.041
Jaw length (9)	0.96	0.76^{-}	0.63-0.92	9.89	0.11	1.42	0.029
Tomiodont length (5)	0.81	1.96	0.93-4.10	0.53	5.89×10^{-3}	0.21	0.17
Tomiodont gap width (5)	0.75	1.60	0.70-3.64	0.76	8.58×10^{-3}	0.29	0.19
Sexual traits							
Carapace length (9)	0.99	0.96	0.92-1.01	99.78	1.10	17.69	0.018
Carapace height (9)	0.92	0.72^{-}	0.56-0.93	37.22	0.41	0.028	0.041
Foreclaw length (9)	0.56	0.89	0.50-1.55	5.50	0.061	0.85	0.10
Pre-cloacal tail length (5)	0.56	0.75	0.27-2.09	10.28	0.12	1.58	0.10

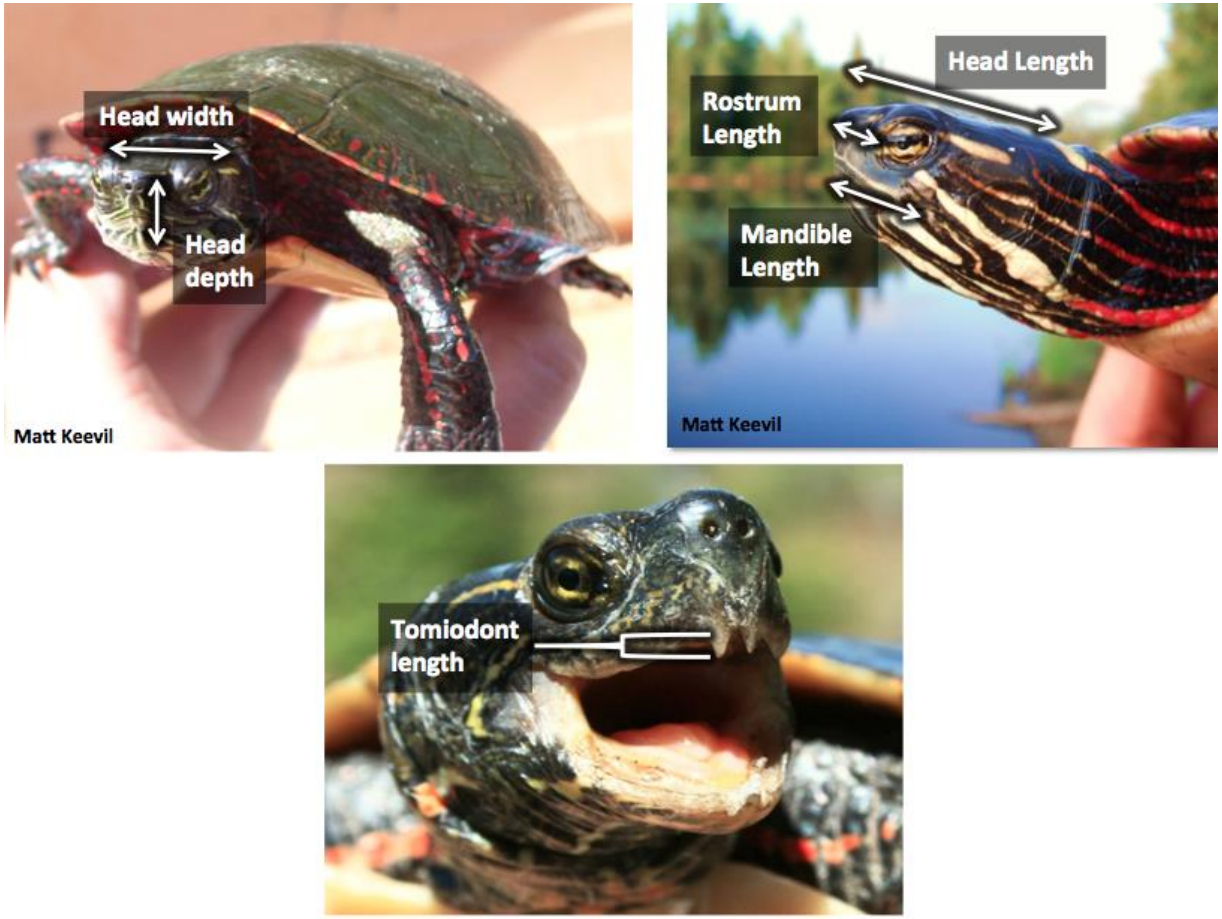

Figure 1.1: Visual representation of cranial morphometric traits measured in mature female, mature male and juvenile Painted Turtles (*Chrysemys picta marginata*) of Algonquin Provincial Park. See Table 1.1 for definitions of traits.

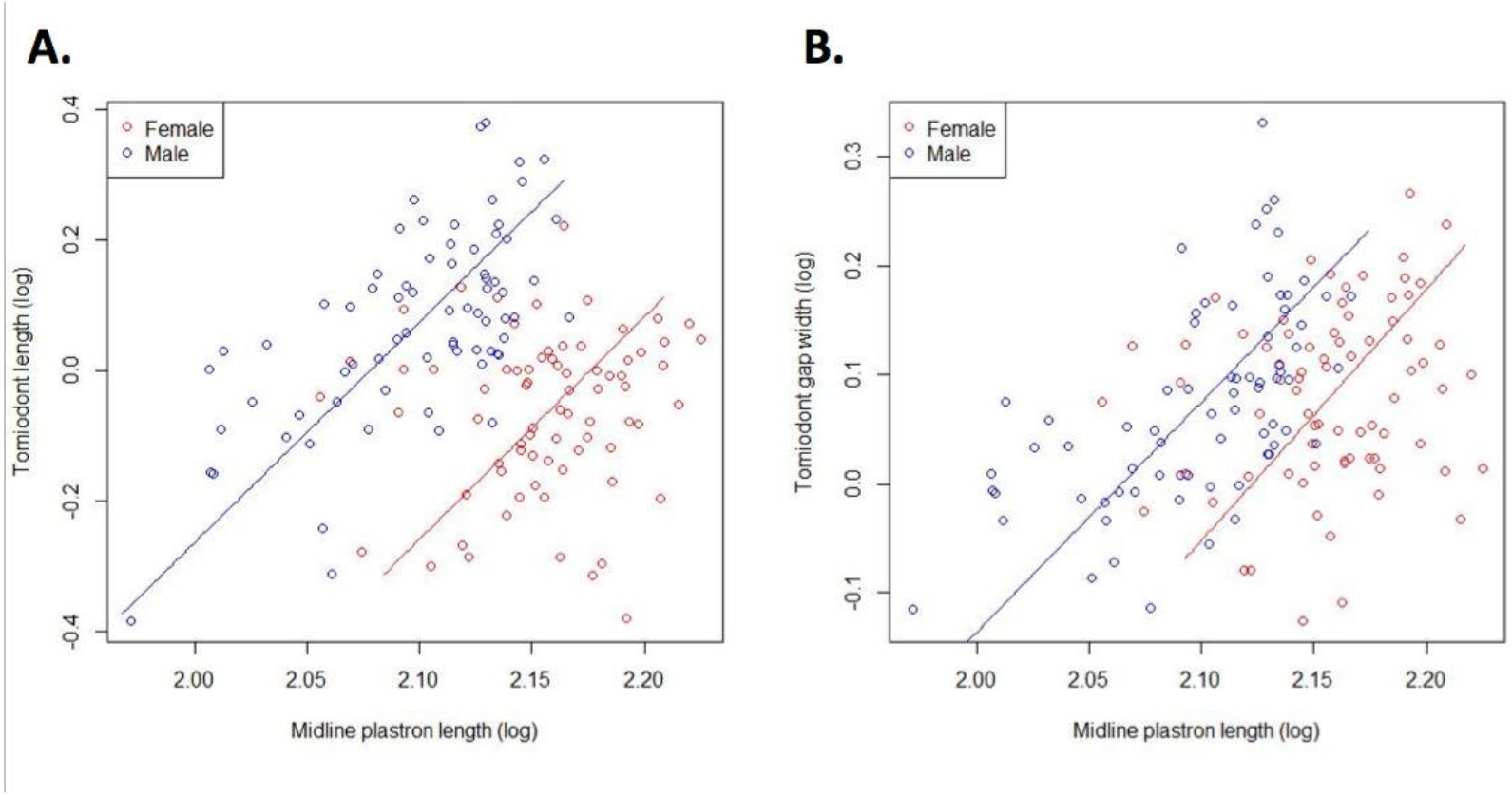

Figure 1.2: Reduced major axis scatterplots of tomiodont morphology and female and male Midland Painted Turtles (*Chrysemys picta marginata*). A. tomiodont length and midline plastron length by sex, log-log scale; B. tomiodont gap width and midline plastron length by sex, log-log scale. Note parallel slopes and difference in elevation (*y*-intercept) in the lines of best fit between males and females.

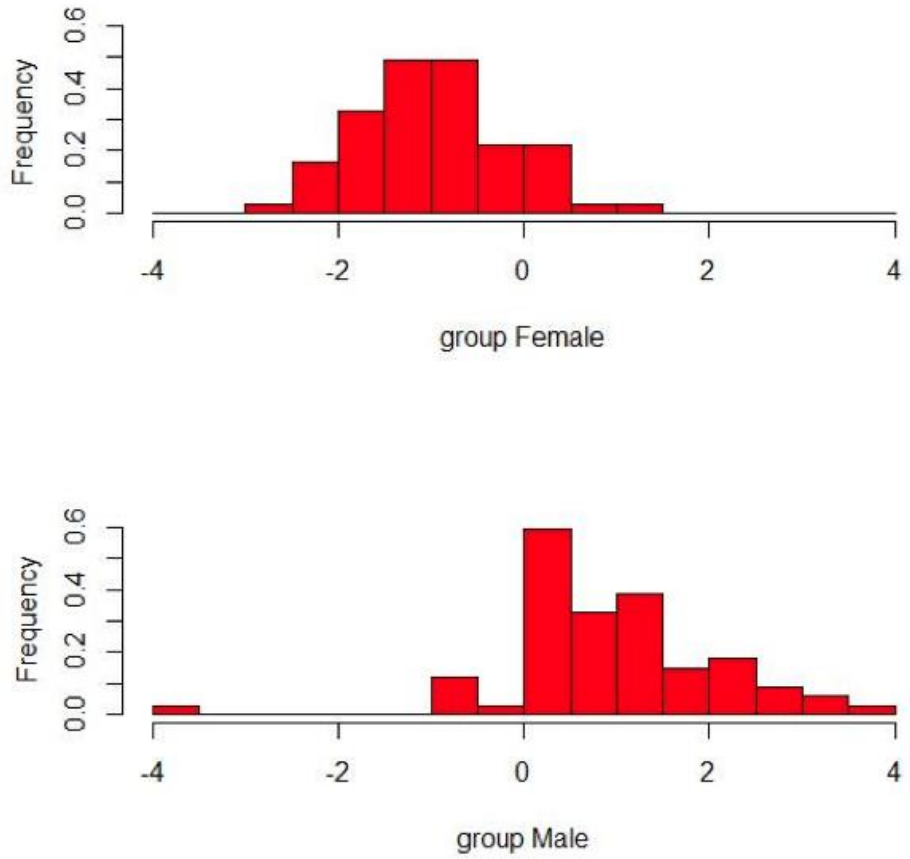

Figure 1.3: Histograms of linear discriminant 1 coefficient values for female and male Midland Painted Turtles (*Chrysemys picta marginata*) from Algonquin Provincial Park. Linear discriminant 1 calculated from the cranial morphometric traits head length, head width, head depth, rostrum length, jaw length, tomiodont length and tomiondont gap width.

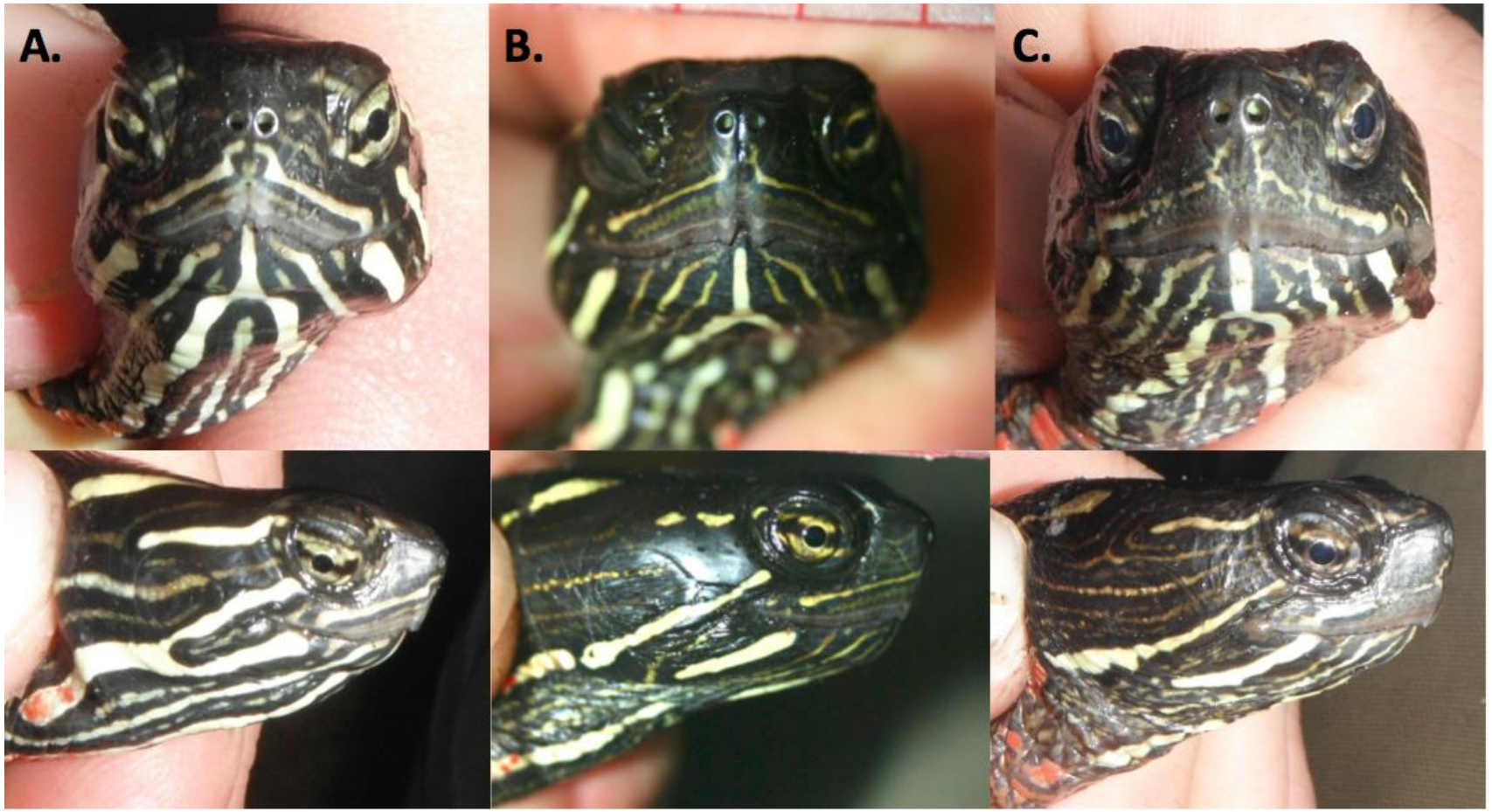

Figure 1.4: Frontal and lateral photos of a juvenile and mature female Painted Turtles of different size classes. Note rostrum-orbital slope, blocky head and relatively blunt snout. A. Painted turtle ID 1480 notch, juvenile (sex unknown), 78.33 mm midline plastron length; B. Painted turtle ID 1502 notch, small female, 123.8 mm midline plastron length; C. Painted turtle ID 0142 notch, large female, 153.4 mm midline plastron length.

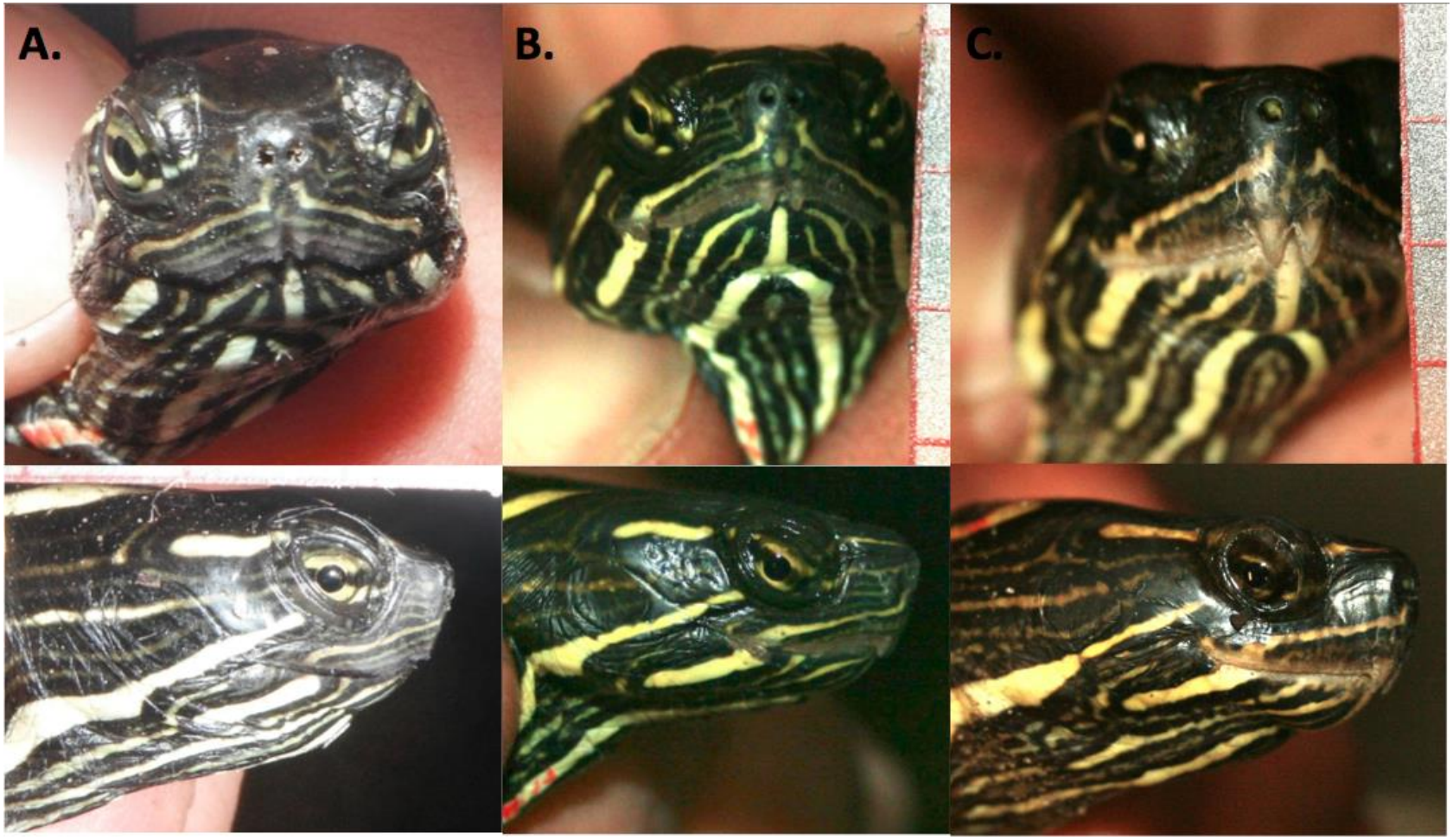

Figure 1.5: Frontal and lateral photos of a juvenile and mature male Painted Turtles of different size classes. Note elongation of the tomiodonts, lengthening of snout and progressively horizontal rostrum-orbital profile with size. A. Painted turtle ID 1190 notch, juvenile (sex unknown), 72.54 mm midline plastron length; B. Painted turtle ID 0103 notch, small male, 103.03 mm midline plastron length; C. Painted turtle ID 1046 notch, large male, 139.4 mm midline plastron length.

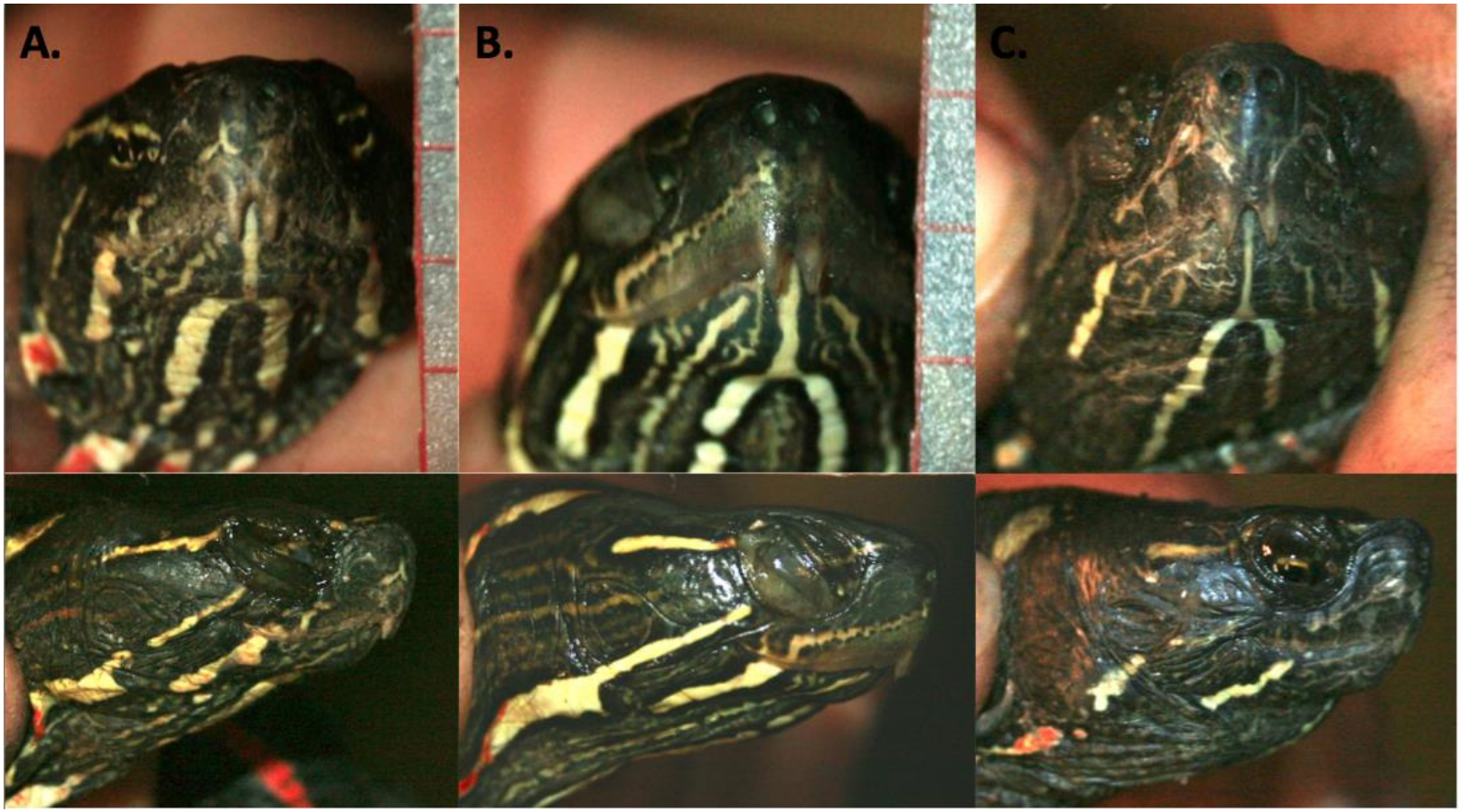

Figure 1.6: Frontal and lateral photos of a mature male Painted Turtles exemplifying extreme cranial morphology phenotype. Note deep premaxillary notch, prominent tomiodonts that overhang lower jaw and elongation of the rostrum. A. Painted turtle ID 1893 notch, male, Wolf Howl Pond, 2.41 mm tomiodont length, 134.7 mm midline plastron length; B. Painted turtle ID 0231 notch, male, Mew Lake, 2.11 mm tomiodont length, 143.0 mm midline plastron length; C. Painted turtle ID 1533 notch, male, Wolf Howl Pond, 2.36 mm tomiodont length, 134.0 mm midline plastron length.

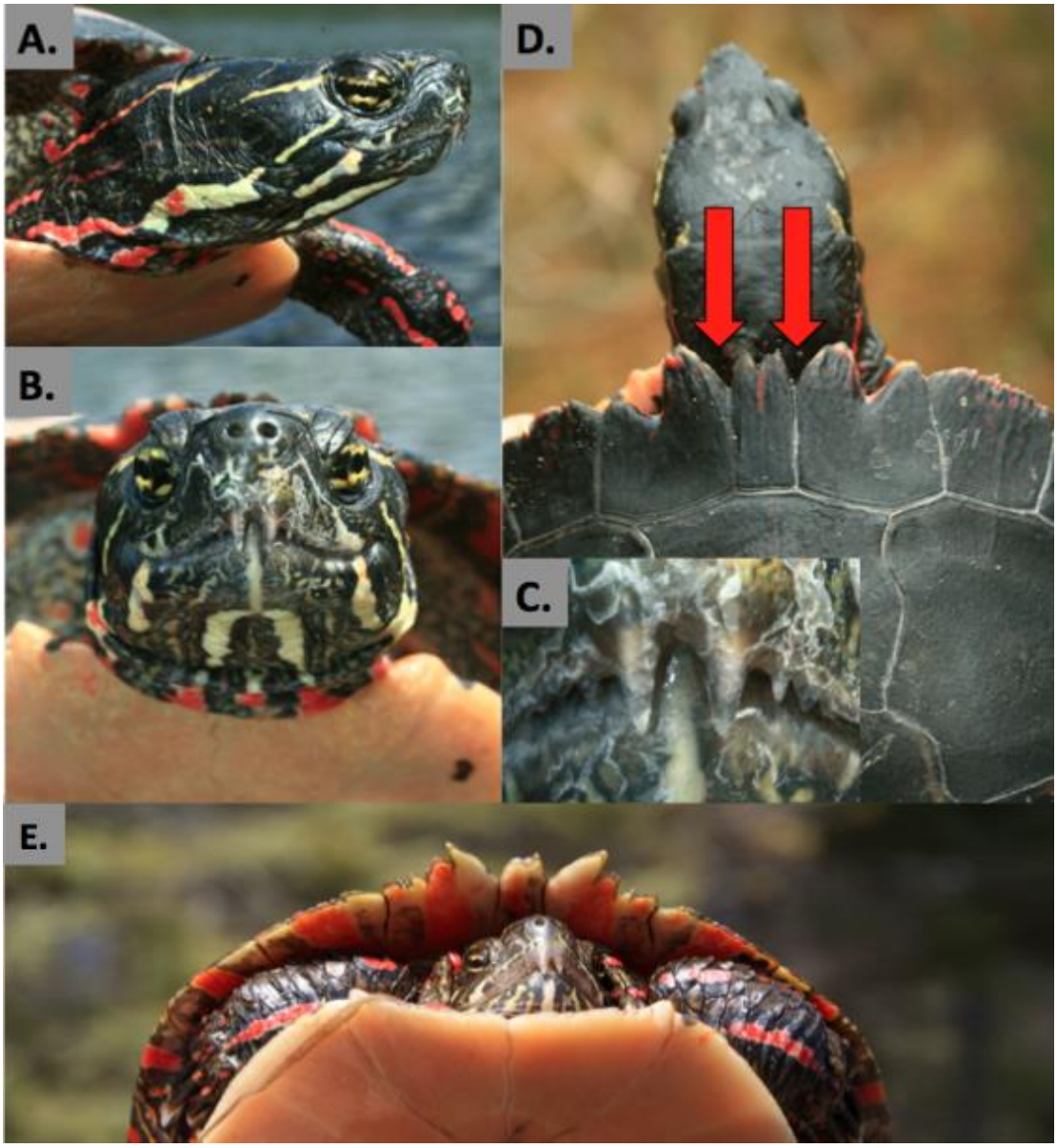

Figure 1.7: Co-occurrence of large tomiodonts and putative anterior carapace dimorphism observed in male Midland Painted Turtle (*Chrysemys picta marginata*) ID 1893 notch. A. Lateral head showing elongate rostrum, tomiodonts overhanging lower jaw and horizontal rostrum-orbital profile. B. Frontal head showing well-defined tomiodonts. C. Enlargement of tomiodonts showing accessory tomium serrations immediately posterior to the tomiodonts. D. Dual pronged projecting cervical scute (nuchal bone), deep natural notches (at arrowheads) on either side of the cervical scute and flared first left and fright right anterior marginals. Note that the notches in the first left and first right marginal are individual identification notches and should not be mistaken for the natural notches. E. Male *C. p. marginata* collected from Estaire (Sudbury district, 46'14"257, 80'41"455), Ontario, Canada. Photo used with permission from Cortney Lee-Comeau and David LeGros (2013).

Chapter II

Sexual coercion and demographics of injuries from conspecific bites in a population of Midland Painted Turtles (*Chrysemys picta marginata*) in Algonquin Provincial Park

"*These little turtles have been described as 'ineffectually irascible' in disposition, although a big one can inflict a painful nip*."

S.A. Minton Jr., in reference to *Chrysemys picta*
Amphibians and Reptiles of Indiana (1972)

"*Many individuals bite when handled and their jaws often are so sharp that they can remove small clean-cut segments from the hand*."

R. Conant, in reference to *Chrysemys picta bellii*
The Reptiles of Ohio (1938)

"*Love hurts, love scars, love wounds, love mars*."
Roy Orbison, "Love Hurts" (1961)

Chapter II: Sexual coercion and demographics of injuries from conspecific bites in a population of Midland Painted Turtles (*Chrysemys picta marginata*) in Algonquin Provincial Park

Abstract: Sexually coercive reproductive tactics are widespread among vertebrate animals. Males may employ specialized structures, often called sexual weapons, to harass, intimidate, and/or physically harm females in an attempt to copulate. Injuries to the head and neck are reported in species with sexually coercive mating systems. Mating tactics of the Painted Turtle (*Chrysemys picta*) are well-recognized as involving an elaborate male courtship display coupled with female mate choice. To the contrary, female *C. picta* in the Algonquin Park (Ontario, Canada) long-term study population have been recorded regularly with injuries on the head and neck indicative of bite wounds, probably inflicted by the tomiodonts (upper jaw cusps) of males during mating. Using a 24-year dataset, I demonstrate *C. picta* population-level trends in soft tissue wounds inflicted by conspecifics. Consistently, adult females experienced more wounding than adult males or juveniles. In addition, larger females have a greater probability of wounding comared to smaller females. Wounding was largely concentrated on the dorsal head and neck of females, consistent with what would be expected from male-female aggression during sexual coercion. Elevated rates of fresh wounding occurred during late summer coincident with the breeding period of *C. picta*. By assessing wound demographics, I provide indirect evidence that the tomiodonts of male *C. picta* inflict injury and are coercive sexual weapons. Further, I propose that male *C. picta* employ alternative coercive mating tactics and contribute evidence toward explaining the sexual dimorphism and functional significance of tomiodonts in *C. picta*.

Introduction

Sexually coercive strategies and structures

Coercive mating strategies used by males include a host of chemical and physical attack structures that are injurious to females pre- or post-copulation and may compromise future female reproductive success (Johnstone and Keller 2000). Some structures, often called sexual weapons or armaments, may be conspicuous (*e.g.*, antlers, horns, and tusks) or subtle and highly specialized for sexual coercion (*e.g.*, toxic seminal fluid, spines on the intromittent organ). Such structures have been documented across a wide diversity of animal taxa. Male *Drosophila* (Chapman *et al.* 1995, Wigby and Chapman 2005), nematodes (Gems and Riddle 1996), and beetles (Das *et al.* 1980) produce toxic seminal compounds that result in short-term increases in female fecundity,

in turn improving male reproductive success, but ultimately reducing female longevity. Genital spines promoting reproductive benefits for males while inflicting harm to females are found in dung flies (Blanckhorn *et al*. 2002) and beetles (Crudgington and Siva-Jothy 2000). Male waterfowl may forcefully grasp the feathers of a female's head and nape with the bill to immobilize her to achieve intromission (McKinney *et al*. 1983). The underwater, terrestrial, and/or aerial harassment of females by males is common in numerous duck species (McKinney *et al*. 1983) and other avian groups, including albatrosses, pelicans, herons, gulls, swallows, and corvids (McKinney and Evarts 1997). Early natural history records (*ca*. 1910) of the Adélie penguin (*Pygoscelis adeliae*) describe displays of sexual coercion by groups of males on a single female (Levick 1915, Russel *et al*. 2012). In a thorough review, Smuts and Smuts (1993) reported widespread sexual coercion in primates and provided examples across diverse mammalian taxa, particularly ungulates, rodents, and pinnipeds. Long-term study of bottlenose dolphins (*Tursiops* sp.) has shown that males display more aggressive tendencies than females, with males biting and inflicting wounds on females during breeding (Scott *et al*. 2005). The resultant scarring serves as an indirect measure of conspecific aggression, which can be related to age and reproductive state of the wound bearer (Scott *et al*. 2005). The mating of sea otters (*Enhydra lutris*) has been described as vigorous, noisy, and brutal (Broseau *et al*. 1975). The wounds of female sea otters have been used as indicators of mating activity (Broseau *et al*. 1975) and are unique enough for individual identification (Gilkinson *et al*. 2007). Coercive tactics of male pinnipeds and sea otters can be so intense that they result in (intraspecific and interspecific) female mortality from overt male aggression (Best *et al*. 1981, Le Boeuf and Mesnick 1991, Miller *et al*. 1996,

Mortensen and Follis 1997, Harris *et al*. 2010). Finally, female sea turtles are subject to aggression and harassment from (single or groups of) males during the breeding period, which is energetically taxing and results in extensive wounding on the flippers, neck, and head of females (Lee and Hays 2004).

Restraint of the head is a seemingly effective means by which to immobilize a mate and would typically place the male in a suitable mounting position. Across taxa, males commonly direct coercive behaviours, such as biting and pinning, at the head and neck of sexual partners: primates (Kummer 1968, Goodall 1986), felids (Rudnai 1973, Lanier and Dewsbury 1976), seals (Siniff *et al*. 1979, Johnson and Johnson 1979, McCann 1982, Alcorn and Buelna 1989, Hiruki *et al*. 1993, Mortensen and Follis 1997), sea lions (intra- and interspecific partners; Miller *et al*. 1996), mustelids (intra- and interspecific partners; Hatler 1970, Foott 1970, Hatfield *et al*. 1994, Harris *et al*. 2010), waterfowl (McKinney *et al*. 1983, McKinney and Evarts 1997), squamates (Noble and Bradley 1933, Secor 1987, Wilms *et al*. 2010), and chelonians (Wood 1953, Legler 1955, Davis and Jackson 1973, Berry and Shine 1980, Comuzzie and Owens 1990, Yasukawa *et al*. 1996, Lee and Hays 2004, Liu *et al*. 2013).

Intersexual aggression and sexual coercion in chelonians

Among freshwater turtles, males of bottom-walking and semi-aquatic species predominantly demonstrate forced insemination of females (Berry and Shine 1980). Coercive mating tactics are often coincident with a larger male body size, limited mobility, and the inability of a female to escape a male even if she is non-receptive (Berry and Shine 1980). Conversely, in aquatic species, male precoital courtship

behaviour and/or nuptial structures are recognized as the principle mating strategy, along with female mate choice (Berry and Shine 1980, but see discussion by Gibbons and Lovich 1990 and Bels and Crama 1994). Members of this latter group typically demonstrate a larger female body size, male nuptial structures (*e.g.*, elongate foreclaws) with associated courtship behaviour, and high mobility (Berry and Shine 1980, Gibbons and Lovich 1990, Liu *et al*. 2013). Thus, for turtle species such as the Painted Turtle (*Chrysemys picta*) with a larger female body size, high mobility, and a free-swimming open water lifestyle, it has been suggested that coercive mating tactics would be unsuccessful (Berry and Shine 1980). However, male aggression may be an effective mating tactic in chelonians if coercive behaviours (*e.g.*, chasing, biting, forced submergence) facilitate female receptivity or acquiescence through demonstration of male dominance or strength (Gibbons and Lovich 1990, Liu *et al*. 2013).

Intersexual aggressive interactions related to breeding have been recorded regularly in chelonians, although most cases are anecdotal and restricted to captivity. In chelonians, sexual coercion may be demonstrated through biting, ramming, chasing, and general harassment (Thomas 2002, Liu *et al*. 2013). While experiencing male coercion, females may demonstrate complacence by retreating into their shell and remaining immobile (*e.g.*, Evans 1953). Alternatively, females may display resistance by trying to evade the pre-copulatory advances of males (*e.g.*, Wood 1953), struggling to free themselves (*e.g.*, Davis and Jackson 1973), or act in a defensive manner such as biting (*e.g.*, Plummer 1977, Kauffman 1992).

In chelonians, biting by males can be an important means of immobilizing a female for breeding (Auffenberg 1964, Sacchi 2003, Liu *et al*. 2013), and may be of

particular importance in highly mobile, fully aquatic species. Male green sea turtles (*Chelonia mydas*) bite breeding females significantly more than non-breeding females, and observations of fresh bite wounds on females are restricted to the breeding season (Comuzzie and Owens 1991). During courtship, female *C. mydas* experience bite wounds all over the body, but especially on the soft tissue regions of shoulders, neck, and around the mouth (Comuzzie and Owens 1991). Biting may also be directed at the shell, limbs, or tail in chelonians (Evans 1953, Legler 1955, Davis and Jackson 1973, Auffenberg 1977, Kauffman 1992, Bels and Crama 1994, Lee and Hays 2004, Schneider *et al*. 2010). Chasing and biting may also drive females to preferred breeding locations (*e.g*., shallow water) where mating commonly takes place (Ernst and Barbour 1972, Harding and Bloomer 1979). Gibbons (1968) reported two observations of male Painted Turtles attempting to restrain a female via biting. Bites from male Sliders (*Trachemys scripta taylori*) directed at females were forceful enough to chip small pieces from the shell scutes (Davis and Jackson 1973). A male *T. s. taylori* was reported to bite a female for as long as five minutes following courtship (Jackson and Davis 1973). Male Wood Turtles (*Glyptemys insculpta*) repeatedly bite at and strike the head of females as females try to move to shallow water to breathe during copulation (Kauffman 1992). Biting may serve in female arousal (Comuzzie and Owens 1990) or as a tactile stimulus (Liu *et al*. 2013). Jackson and Davis (1972) proposed that the function of male biting is to promote immobility of the female, particularly when directed at the female's head.

Another coercive mating behaviour exhibited by male chelonians is shell ramming, shell clapping (Lui *et al*. 2013), or shell clattering (Kramer 1984, 1989). Evans (1953, 1968) reported male Box Turtles (*Terrapene carolina*) making lunging bites and

delivering repeated blows to females with their anterior carapace that lasted for over an hour. Similarly, male *Terrapene ornata* have been observed in lengthy bouts of biting and plastral ramming with females (Brumwell 1940). In the Marginated Tortoise, *Testudo marginata*, male mounting success is highly correlated with the number of bites and rams given to females before mounting (Sacchi *et al*. 2003). The shell butting of males and females can be forceful enough to produce loud sound (Brown 1974, Kramer 1984, 1989), and may be audible up to 100 m away in large tortoises (Auffenberg 1977). Males may physically displace females during bouts of coercion by dragging or forceful ramming (Evans 1953, Auffenberg 1977, Kramer 1986).

Research direction

In keeping with their aquatic lifestyle, male *C*. *picta* are reported to court females with a non-aggressive display during the breeding season (Taylor 1933, Cagle 1954, Ernst 1971*a*, Berry and Shine 1980, Ernst and Lovich 2009). However, *in situ* observations from the long-term Arowhon study population in Algonquin Provincial Park have documented male-female agonism. Wounds on the head and neck have been recorded regularly in female *C*. *picta* in the Arowhon population, consistent with sexual coercion and biting patterns in other animal taxa. These observations provide a line of evidence that coercive mating tactics may be present in the Arowhon *C*. *picta*.

The objective of the research presented in Chapter II was to quantify the frequency and demography of bite wounds on *C*. *picta* in the Arowhon population, Algonquin Provincial Park to test the hypothesis that sexually coercive mating tactics are present in *C*. *picta*. I examined wounding demographics, an indirect measure of sexual coercion, in

C. picta from long-term database records (1990-2013). Records were evaluated for wound presence or absence, wound condition (new or old), and wound location (head or body). Wounding was compared among sexes, size classes, and seasons. If sexual coercion is present in the Arowhon *C. picta* population, then I would expect, i) a higher incidence of wounding on mature female turtles compared to adult male and juvenile conspecifics; ii) wounding concentrated on the head and neck of females; and, iii) seasonal wounding patterns consistent with putative breeding activity.

Methods

Study population and site

The Arowhon study population of *C. picta* occurs at three adjacent wetlands, Wolf Howl Pond, Wolf Howl Pond East, and West Rose Lake (45°34'N, 78°41'W), Algonquin Provincial Park, Ontario, where monitoring of population demographics and reproduction has taken place annually since 1978 (R.J. Brooks). Population size estimates based on mark-recapture study approximate 400 adults at the three sites combined (Samson 2003). The *C. picta* at the Arowhon sites are found at varying population densities: Wolf Howl Pond 128.6 turtles/ha, Wolf Howl Pond East 17.9 turtles/ha, West Rose Lake 16.3 turtles/ha (S. Sanders and M. Keevil, unpublished data). The high *C. picta* density at Wolf Howl Pond is likely due to relatively good habitat quality, the small size of the water body, and access to nearby nesting habitat. The sex ratio of the adult population is strongly female biased (3.44:1, female:male) (Samson 2003). The Arowhon population of *C. picta* is sympatric with Snapping Turtles (*Chelydra serpentina*), and rarely, Blanding's Turtles (*Emydoidea blandingii*). A complete site description can be

found in Schwarzkopf and Brooks (1985). Painted Turtles were captured by canoe or baited hoop trap and transported and processed in the lab at the Algonquin Wildlife Research Station (AWRS, Algonquin Provincial Park, Ontario, Canada).

Wounding evaluations and records

Consistent with the long-term study, remarks on injuries and abnormalities were recorded (1990 onward) and eight body morphometrics were measured using Vernier calipers (to the nearest 0.01 cm). Wounding records vary in quality between years based on sampling effort and the detail of the remarks recorded for each turtle. Within the 24-year dataset, two periods represent years with directed wound monitoring: 2003-2007 (E. Hughes) and 2013 (P. Moldowan). During 1990-2012, multiple observers evaluated wounding. In 2013, I evaluated all turtles for wounds and documented wounds with detailed remarks on wound condition, location, measurements and photographs. Remarks on wounding from 1990-2012 were largely restricted to the spring (May-June) sampling period. In 2013, turtles were evaluated for wounds during the spring (May-June) and late summer (August-September) consistent with the breeding periods of the species (Gibbons 1968, Mitchell 1985*a,* 1985*b*, Ernst and Lovich 2009).

A total of 8811 capture records (1990-2013) were evaluated from the long-term database. Of these capture records, 7088 (~80%) were accompanied by remarks of suitable quality to evaluate the presence or absence of wounding and wound condition (Table 2.1). Evaluations were restricted to wounds on the soft tissue of the head, neck, limbs, and tail (*i.e.*, traumatic injuries to the shell, limbs, or tail were not considered as these are unlikely to be caused by conspecifics). Wound locations were further sub-

divided into dorsal head/neck, throat/ventral neck, chin/jaw, lateral head/neck, eyelid, an ambiguous head/neck location, limb, and tail. Using keywords recorded in the remarks, wounds were classified as new or old. Wounds were considered new when described as "new", "fresh", "red", "scab", "sore", "cut", "open", or if "blood" was present. Old wounds were recognized as "old" "scar", "white", "black", or "dark". Wounds were classified as ambiguous when either the wound condition or location was not clearly stated (*e.g.*, the remark "bite marks on lower neck" is ambiguous with respect to wound condition and would location because it is unclear regarding wound freshness and whether the wound is on the lateral or ventral neck).

Statistical analyses

All statistical analyses were completed in *R* statistical software (R Development Core Team 2013).

Wounding by sex: Turtles were classified as adult female, adult male, or juveniles of unknown sex. Sex was discerned by body size, secondary sexual characters (*e.g.*, elongate foreclaws and tail in males), and/or observations of reproductive activity (*e.g.*, gravidity, nesting in females). In the Arowhon population, males demonstrate foreclaw elongation and maturity at approximately 85-95 mm midline plastron length, whereas females mature between approximately 121-142 mm midline plastron length (Samson 2003). A Kruskal-Wallis rank analysis tested for a difference between the mean proportion of wounded adult females, adult males, and juveniles across all years (1990-2013). Further, post-hoc analysis using Wilcoxon (rank signed) tests examined pairwise

comparisons between adult females, adult males, and juveniles for differences in wounding proportions across all years (1990-2013). To examine wounding patterns among adults, a Fisher's exact test was used to test for differences in proportions of females and males with wounds for each year. In addition to null hypothesis significance testing, the magnitude of wounding was assessed between adult females and adult males using effect size statistics. As a measure of effect size, an odds ratio (OR; as per Nakagawa and Cuthill 2007) was calculated to quantify the difference in wounding between adult females and males in each year. An OR=1 indicates equal wound proportions between males and females, OR>1 represents female-biased wounding, and OR<1 indicates male-biased wounding. An OR could not be calculated if zero individuals within a group were wounded (as was the case for males in some years).

Wounding by size: Body size (midline plastron length, mm) was used as a continuous variable with respect to wounding patterns. For adult females, adult males, and juveniles, logistic regression was used to test whether presence or absence of wounds was related to size (midline plastron length, mm). For adult females and adult males, a multivariate logistic regression was conducted to test for an interaction of body size and sex with wounding. Midline plastron length, sex and a midline plastron length-sex interaction were included as explanatory variables, and presence or absence of wounds as the response variable. Logistic regression was restricted to the 2013 spring wounding records because of the highly rigorous evaluation of wounds in this year (see *Wounding evaluations and records*).

Wounding by body region: Data on wound location in adult female and adult male *C. picta* were pooled and grouped according to the eight body locations (outlined above). For each of the 24 years, the proportion of wounds at each body region location was calculated and averaged. A Kruskal-Wallis test evaluated the null hypothesis that there was no difference in mean wound (ranked) proportions among body regions. Effect size, represented as Cohen's *d* (Eq. 1 in Nakagawa and Cuthill 2007; also see Cohen 1988), was calculated from pairwise comparisons between wounding locations in order to 1) evaluate the magnitude of [differences in] wounding between locations and 2) assess the precision of the estimate of the magnitude of wounding (Nakagawa and Cuthill 2007).

Wounding by season: In 2013, turtles were captured during May (immediately post-brumation) and June (pre-nesting) and assessed for wounds. Follow-up wounding evaluation took place through repeated sampling in late summer, during August and September. During both sampling periods, condition and location of wounds were recorded and a summary was made from compiled records for turtles that were caught multiple times in a season. For turtles caught in both spring and late summer, it was of interest to know whether prevalence of wounding differed between the spring breeding and late summer breeding periods. The number of individuals with spring wounds only, late summer wounds only, both spring and late summer wounds, and no wounds in either season were compared using a Kruskal-Wallis test.

Results

Wounding by sex: From 1990 to 2013, an average of 16.2% of females (n = 24 years, SD = 0.09, 95% CI = 0.03), 7.7% of males (N= 24 years, SD = 0.05, 95% CI = 0.02), and 2.8% of juveniles (n = 23 years, SD = 0.07, 95% CI = 0.03; note that no juveniles were captured in 1996) were observed with wounds. The proportion of wounded individuals differed significantly between adult females, adult males, and juveniles across the 24 years (Kruskal-Wallis X^2= 42.76, df = 2, $p < 0.0001$). Juveniles did not demonstrate wounding in most years (18 of 22 years, 82%). The mean proportion of females with wounds was significantly greater than that of males (Wilcoxon test, $W = 504$, $p < 0.001$; Figure 2.1) and juveniles (Wilcoxon test, $W = 556$, $p < 0.0001$) from 1990-2013. Males demonstrated significantly higher wounding rates than juveniles when pooled across all years (Wilcoxon test, $W = 94$, $p < 0.001$). The proportion of females with wounds was consistently greater than the proportion of males with wounds, except in the years 1990 and 1993 when no difference in wounding was observed between males and females (Fisher's exact test, Figure 2.1, Table 2.2). On average, the proportion of wounded females was 2.6 times greater than the proportion of wounded males (Table 2.2, Figure 2.2). Females were up to 6 times more likely to have wounds than males (Table 2.2). During periods of directed wound study (2003-2007 and 2013), 20-45% of females were wounded, whereas 8-20% of males had wounds over the same period (Table 2.2). The high sampling effort in 2013 resulted in the greatest number of wounds observed in males and females and the greatest proportion of wounded individuals of each sex.

Wounding by size: In adult females, the presence of wounds was associated with larger body size. Larger females had a greater probability of bearing wounds in both the spring ($z_{306} = 3.871$, $p < 0.0001$) and late summer ($z_{115} = 3.179$, $p < 0.001$) breeding periods (Figure 2.3). In contrast, male body size did not predict the presence of wounds in either the spring ($z_{63} = 1.582$, $p = 0.11$) or late summer ($z_{38} = 1.299$, $p = 0.19$; Figure 2.4). No interaction between size and sex was found with respect to wound probability ($z_{370} = 0.166$, $p = 0.87$). Wounding was not associated with body size in juveniles in either the spring ($z_{42} = 0.770$, $p = 0.44$) or late summer ($z_{10} = 0.692$, $p = 0.49$; Figure 2.5).

Wounding by body region: Differences in wounding were assessed for the head (including head and neck) and body (including limbs and tail). Wounds were observed in significantly greater proportions on the head compared to the body across all 24 years ($W = 624$, $p < 0.0001$). The proportion of wounds among body regions differed significantly ($H = 94.64$, $df = 7$, $p < 0.0001$). Among wounded individuals, approximately 88% ± 5% (95% CI) had head injuries, whereas approximately 12% ± 5% (95% CI) had body injuries. Wounding was significantly greater on the dorsal head and neck relative to all other head and body regions (Table 2.3, Table 2.4, Figure 2.6). Wounding to the dorsal head and neck was observed 2-3 times more frequently than wounding to other body regions (Table 2.3, Table 2.4, Figure 2.6). The proportion of wounds on the throat and ventral neck was significantly greater than that on the limbs and tail (Table 2.4, Figure 2.6).

Wounding by season: Of the 154 turtles caught both in the spring and late summer of 2013, 12% (n = 19) had wounds in the spring only, 25% (n = 39) had wounds in the late summer only, 19% (n = 29) had wounds in both the spring and late summer, and 44% (N = 67) did not exhibit wounding in the spring or late summer (H = 3, df = 3, p = 0.39). Among those turtles that had wounding in both spring and late summer, 90% (n = 26) of the late summer wounds were different than the spring wounds (*i.e*., different location or new wound condition), indicating that wounds were acquired post-spring. The number of females with both new and old wounds in the late summer increased compared to the spring (Figure 2.7). No males were observed with new wounds in the late summer (Figure 2.7).

Descriptive remarks on wounds

Fresh wounds were easily recognized by the presence of blood, inflammation, and the visible underlying raw, red or pink tissue. Occasionally, the fresh wounds clearly resembled two shallow parallel gashes (Figure 2.9, Figure 2.10). The width between these gashes approximated that of the distance between the tomiodonts of *C*. *picta* (see Chapter I), providing compelling evidence that the tomiodonts of a conspecific are responsible for inflicting the wounds. These fresh wounds are discrete and often obscured by the intricate ventral head pattern or dark dorso-lateral head colouration of *C*. *picta*. Scabbing is characterized by a rough patch of brown-grey tissue overlying the wound and can be observed 2-7 days following the initial injury. After approximately 10-14 days, the scab is sloughed off to reveal conspicuous white scar tissue. During scar healing, the tissue surrounding the wound site appears glossy and contrasts sharply with the surrounding

dark skin of the dorsal/lateral head and neck. Scar contrast is not as strong on the vermiculated yellow and black patterning (symphyseal stripe) of the throat. White scarring appears to gradually darken over the course of a month during the active season to become indistinguishable in colour from the surrounding tissue (Figure 2.11, Figure 2.12). Most scars are roughly circular in shape and appear to heal from the centre with darkening of the skin (re-pigmentation/re-melanisation) radiating outward. This pattern results in wounds taking on a ring appearance late in the healing process (Figure 2.11). In rare cases, scarring can still be discerned as irregular or gouged skin even when the wound area was completely colonized by melanophores (Figure 2.8B). Numerous females, particularly larger and older individuals, have loose, smooth, wart-like skin on the nape of the neck, resembling heavily scarred or callused tissue (Figure 2.8D). In these cases, the dorsal neck skin is often a uniform black colour and interrupts the characteristic red and yellow neck striping (occipital blotches) characteristic of *C. p. marginata*.

Discussion

I assessed wounding demographics in the *C. picta* population at the Arowhon sites in Algonquin Provincial Park in relation to sex, individual size, body location, and seasonality using a 23-year dataset. I found that larger adult females had the highest incidence of wounding, that wounds were mostly on the dorsal head and neck, and that wounding occurred most frequently in late summer. These data provide a line of evidence that coercive mating tactics are present in the Arowhon *C. picta* and thereby support my hypothesis of sexual coercion in *C. picta*.

Wounding by sex

The presence of soft tissue wounds was relatively low in the population at large, with approximately 16% of females and 7% of males bearing wounds across all years. I found strong support for my prediction that wounding was female-biased. Females typically experienced two to three times, and up to six times, the number of wounds in a given year compared to males (Table 2.2).

Inference about wounding in juveniles is difficult because of low annual juvenile captures and the inflated (and misleading) proportions of wounded juveniles when wounding does occur. For instance, in 1991, 2009, and the late summer of 2013, the proportion of juveniles exhibiting wounds was high at 20%, 10%, and 30%, respectively. However, with only five (1991) and ten (2009 and late summer 2013) juveniles captured in these years, even a single wounded individual constitutes a considerable proportion of the sample.

Wounding by size

Body size was an important predictor of the presence of wounds in adult female *C. picta*, but not in males or juveniles in 2013. It may be that larger (and/or older) female *C. picta* are preferred mates given their high fecundity (Pearce *et al*. 2001, McGuire *et al*. 2011) and thereby experience greater male harassment. Males have the potential to gain higher reproductive fitness by preferentially mating with large females. While larger females may be more desirable, they may also be better able to resist male harassment. If

this is true then males may employ coercion, rather than titillation, with larger more desirable females in an attempt to maximize reproductive fitness.

Wounding by body region

Consistent with my prediction, Arowhon *C. picta* demonstrate wounding concentrated on the head, particularly the dorsal head, dorsal neck (nape), throat, and ventral neck, compared to the body (Figure 2.6). Wounding to the head and neck was significantly greater than that to other body regions (*i.e.*, limbs and tail), a trend consistent across all years. Across diverse vertebrate taxa, females exhibit injuries to the head and neck caused by the coercive mating attempts of males (Le Boeuf and Mesnick 1990, Smuts and Smuts 1993, Wilms *et al*. 2010). The injuries sustained by females from male coercion can occur in greater numbers than injuries from other causes, such as predation and accidental wounding (Hiruki *et al*. 1993). Soft tissue wounding on the head and neck of the Arowhon *C. picta* is inconsistent with predator attacks in form and severity. If a predator gained access to the head of a turtle, the results would almost certainly be fatal. Further, the idea that the soft tissue wounding seen on the Arowhon *C. picta* may be attributed to predators does not explain the observed sex-bias in wounding, unless females are more susceptible to predators (a prediction not supported by Arowhon population annual survivorship data, Samson 2003). Accidental injury seems an unlikely cause of wounding, especially to the head and neck. In addition, leeches are an unlikely cause of wounds or scarring; when leeches are removed from areas of the body where they commonly congregate (*e.g.*, base of the tail, inguinal pockets of limbs), such skin abrasion is not observed.

Wounding by season

In contrast to males, females demonstrated a greater presence of both new and old wounds in the late summer compared to the spring. Observations of turtles with wounds in the spring only and non-identical spring and late summer wounds indicate that injuries are capable of completely healing within a single active season (early May to late September in Algonquin Park). Photographs of wounds taken during the spring and late summer sampling periods demonstrate considerable or complete healing over the active months (Figure 2.8). Spring is purported to be the primary breeding period for Painted Turtles (Sexton 1959; Gibbons 1968; Krawchuk and Brooks 1998; Ernst and Lovich 2009), although several observations (Taylor 1933) and reproductive physiology studies have demonstrated reproductive activity in autumn, including enlarged testes (Gibbons 1968), elevated sperm production (Gist *et al*. 1990), and presence of sperm in the female reproductive tract (Gist *et al*. 1990). The primary breeding season for the Algonquin *C. picta* has not been confirmed, although reproductive behaviour has been observed in both the spring and late summer.

The importance of directed study in wound evaluation

The rate of observed wounding is highly variable across years, likely due in large part to researcher search effort. In years where wounding was not under direct study, the proportion of females with wounds and the proportion of males with wounds often do not differ notably; however, it is clear that in years with directed study (as in 2003-2007 and 2013), the proportion of females bearing wounds greatly exceeds that of males (Table 2.2, Figure 2.1). Not surprisingly, the highest number of wound observations and

proportion of turtles with wounds were made during years when wounding was under direct study (Table 2.2, Figure 2.1). A post-hoc analysis showed a significant difference in the observed proportion of wounded turtles in years with high and low wound sampling effort (Kruskal-Wallis $X^2 = 11.1$, df = 1, $p < 0.001$). It seems that wounds are easily overlooked and, as a result, are unreported unless under direct scrutiny. This potential under-reporting highlights the importance of specific study, as opposed to casual observation, in order to quantify and assess patterns in wounding. If anything, wounding estimates are conservative. The discrete nature of wounds, the effectiveness with which a turtle conceals its soft tissue (by retracting their heads, limbs, and tail into their shells), and the attention of the observer, all contribute to whether a wound is overlooked. It is noteworthy that biting did not always result in external wounds (see Chapter III), suggesting that wounding estimates may be conservative. Similarly, Kramer (1989) reported for *Pseudemys nelsoni* and *P. concinna* that conspecific bites did not result in wounds (note that *P. concinna* does not bear tomiodonts).

Male wounding and intrasexual aggression in chelonians

Although female *C. picta* displayed more wounds than males, males in the Arowhon population still incurred notable wounding, which may be a result of intrasexual aggression. Male chelonians demonstrate more aggressive behaviours than females, with males directing aggression both inter- and intrasexually. Open mouth displays, lunging, biting, frontal ramming, and chasing are important for winning male-male fights, for intersexual reproductive activities, and for establishing a high rank in social hierarchy in chelonians (Auffenberg 1977, Barzilay 1980, Kauffman 1992). Male

Wood Turtles (*Glyptemys insculpta*) will bite for several minutes during male-male combat, but despite these vigorous fights, wounding is rare (Kauffman 1992).

In contrast, female chelonians rarely bite or demonstrate aggressive tendencies (Auffenberg 1977, Kauffman 1992). A noteworthy exception includes sea turtles; unreceptive females can inflict severe wounds on suitor males (Booth and Peters 1972, Lee and Hays 2004). Aggression towards males is significantly greater in breeding female green sea turtles compared to non-breeding females (Comuzzie and Owens 1990). In other turtle species, non-receptive females may also respond aggressively to male advances (*e.g.*, *Apalone mutica*, Plummer 1977; *Glyptemys insculpta*, Kauffman 1992; and *Podocnemis erythrocephala*, Schneider *et al*. 2010). Female sea turtles (Booth and Peters 1972) and kinosternids (Mahmoud 1967) may also demonstrate non-aggressive nipping of males during courtship and copulation.

Although rare, aggressive interactions in chelonians have been observed outside of a reproductive context, such as open mouth gaping and biting during basking in *Actinemys marmorata* (Bury and Wolheim 1973) and *Chrysemys picta* (Bury *et al*. 1979).

Male coercion and female cost

Males may direct an array of coercive behaviours toward females, including chasing, intimidation, infanticide, and physical attack (Smuts and Smuts 1993). Ultimately, females experience high costs and can incur serious fitness consequences in terms of energetics and future reproductive potential because evading or struggling to resist males is expensive (Arnqvist and Nilsson 2000, Crudington and Siva-Jothy 2000, Shine *et al*. 2003, Arnqvist *et al*. 2004). For example, polyandrous female *Lacerta* lizards

(*L. vivipara*) produce larger brood sizes but incur more mating injuries and scarring from males compared to monogamous females (Fitze *et al*. 2005). Further, persistent male harassment can displace females from optimal foraging areas (Magurran and Seghers 1994), increase predation risk (Rowe 1994), induce chronic stress (Smuts and Smuts 1993, Muller *et al*. 2007), cause the loss of offspring through infanticide, and otherwise occupy time necessary for other activities (Daly 1978, Mallory and Brooks 1978, Labov *et al*. 1985, Smuts and Smuts 1993, Rowe *et al*. 1994, Jennions and Petrie 2000). Males may injure females during physical restraint, struggle and mating resistance (Clutton-Brock and Parker 1995, Johnstone and Keller 2000, Crudington and Siva-Jothy 2003, Head and Brooks 2005). Male *C. picta* do not offer direct reproductive benefits to females in the form of nuptial gifts or parental care. Given a lack of apparent benefits to females and the potential costs associated with mating, it is clear why females would be reluctant to mate at every opportunity. However, resisting coercive mating attempts may be even more costly for a female than mating itself, especially if she experiences repeated harassment and injury.

In addition, female *C. picta* may still incur costs long after the breeding season. Injuries from males may become infected and females must invest resources for healing even outside of the breeding period, and indeed females in the Arowhon population bear wounds year-round. Basking and feeding activities are critical in the late summer and early fall when females begin the first half of egg development (Gibbons 1968, Ernst 1971*b*, Callard *et al*. 1978, Congdon and Tinkle 1982, Congdon and Gibbons 1990, Krawchuk and Brooks 1998, Rollinson and Brooks 2007). Considering the elevated rate of injury in the late summer, energetic investment into healing and the avoidance of

males may curtail resource allocation away from reproduction in this already thermally and energetically constrained northern *C. picta* population (Koper and Brooks 2000, Rollinson and Brooks 2007).

Wound healing and energetics

Turtles emerged from winter dormancy (first week of May) with old wounds, presumably sustained during the previous summer. Due to resource limitation and periods of extremely reduced metabolism (6-7 months winter dormancy and 1-2 months active but not feeding), it is suspected that Algonquin *C. picta* invest very little into healing during winter. Reduced temperatures slow wound healing in reptiles, as observed with garter snakes, *Thamnophis sirtalis* (Smith *et al*. 1988), and caiman, *Caiman yacare* (Pressinotti *et al*. 2013). Thus, wound healing is largely restricted to the short active season (May-September) in the Arowhon population. Personal observations suggest that healing occurs more rapidly during the late active season (August-September) compared to the early active season (May-June), possibly when the turtles are in an increasingly positive energy balance. Accelerated healing late in the active season seems likely given that individuals have paid-off any potential overwinter energy debt, females are post-oviposition, and foraging and basking activity is maximized. Repeated sampling and seasonal captures can inform the timing of injury (Figure 2.12) and rate of healing (Figure 2.10, Figure 2.11).

Biting as a male coercion tactic in turtles

In sexual coercion, biting can serve in pre-copulatory intimidation or the immobilization of a mate. Successful copulation is only possible if a female is receptive or coerced into mating. Biting in chelonian courtship is not surprising, but such behaviours have only been reported sporadically across taxa (Jackson and Davis 1972, Liu *et al*. 2013). Biting during courtship appears to be a conserved behaviour in chelonians, although secondary strategies, such as foreclaw display, may have evolved as an alternative means by which to achieve female quiescence for mating (Jackson and Davis 1972, Liu *et al*. 2013). A male mating tactic involving biting and coercion can reasonably co-exist with that of courtship and female mate choice. Evidence in sliders (*Trachemys* sp.) suggests that males undergo an ontogenetic shift in mating tactic from courtship to coercion (Thomas 2002). Larger individuals of *Trachemys* (Hites *et al*. 2013) and *Pseudemys* (Kramer 1986, 1989) have a greater biting propensity.

It has been proposed that sexual coercion would be an unsuccessful mating tactic in aquatic open-water turtles (such as *Chrysemys* sp.) because i) females are often the larger sex, ii) females can (supposedly) easily evade male advances, and iii) observations of secondary display structures used in elaborate male courtship indicate female mate choice (Berry and Shine 1980). In contrast, my wound data suggest that sexual coercion is present in a highly aquatic chelonian species and that this tactic may be much more important to the species' biology than presently appreciated.

Future directions and conclusions

The wounding sex-bias, location-bias, timing and healing patterns I observed raise a number of questions for future research projects. Firstly, further study to confirm the primary breeding season of Arowhon *C. picta* is necessary. This could be accomplished through continued field observation and cloacal swabbing to detect the presence of sperm in the female reproductive tract throughout the active season. The re-evaluation of wound photos and descriptions could be used to develop a rank system of wound condition to enable a more rigorous assessment of healing patterns. In addition, the state of an injury, whether fresh or in a stage of healing, could more accurately inform the timing of the injury and thereby potential mating (as used by Scott *et al*. 2005 in the study of sexual coercion in the bottlenose dolphin, *Tursiops* sp.). Future workers could examine wounding and clutch size or female body condition to evaluate the costs associated with injury. Examining the database remarks about individual females to evaluate their wound history would be of particular interest (*i.e*., are some females attacked more than others for reasons other than size?).

Future researchers should continue to take detailed data on wounds, including wound condition, size, location, and photographs. Although wound evaluation was restricted to the long-term Arowhon *C. picta* population, it is clear that conspecific wounds are present on females and males from other Algonquin sites, including Bat Lake, Broadwing Lake, Davie's Bog, Lake of Two Rivers (Old Airfield), Mew Lake, Pog Lake, Whitefish Lake, and captures along the Highway 60 corridor. Other researchers working with *C. picta* have reported wounding present in populations outside of Algonquin (C. Davy, Pinery Provincial Park, Ontario; J. Riley and J. Baxter-Gilbert,

Burwash, Ontario; J. Rowe, Beaver Island, Michigan). Suffice to say, conspecific wounding does not appear to be unique to the Arowhon *C. picta* population, Algonquin Provincial Park, and deserves attention in other location where the ecology of the turtles may differ considerably (growing season length, wetland productivity, population sex ratio, population density, *et cetera*).

Chelonians appear to have some sexually dimorphic traits that serve in overcoming the inherent difficulty associated with mating when one has a shell (*e.g.*, male plastron concavity). Of the male dimorphic traits that assist in mounting and mating, none are clearly coercive in nature. I proposed that the tomiodonts of male *C. picta* are sexual weapons used to subdue females for mating (Chapter I). By assessing wound demographics I have provided indirect evidence that the tomiodonts of male *C. picta* inflict injury and, by their very nature, are coercive. Thus, I have established two lines of evidence that sexual coercion is present in the Arowhon population *of C. picta*: sexually dimorphic tomiodonts in males that appear to function as a sexual weapon, and the prevalence of wounding on the head and neck of females. In Chapter III, I will tie these two observations together by using behavioural trials to evaluate the functional significance of the tomiodonts in the mating tactics of male *C. picta* in Algonquin Provincial Park.

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Table 2.1: Annual total number of Painted Turtle (*Chrysemys picta*) captures from the Arowhon population, Algonquin Provincial Park, compared with number of individuals with database remarks relevant for wounding evaluation. In 2013, "S" represents spring sampling (May and June) and "LS" presents late summer sampling (August and September).

Year	No. turtle captures	No. turtles with remarks	% with remarks
1990	206	134	65.05
1991	204	121	59.31
1992	270	161	59.63
1993	287	114	39.72
1994	288	117	40.63
1995	297	153	51.52
1996	288	165	57.29
1997	262	146	55.73
1998	325	247	76.00
1999	367	183	49.86
2000	401	205	51.12
2001	366	318	86.89
2002	439	409	93.17
2003	466	451	96.78
2004	494	471	95.34
2005	495	486	98.18
2006	427	418	97.89
2007	427	412	96.49
2008	455	437	96.04
2009	268	187	69.78
2010	339	322	94.99
2011	434	429	98.85
2012	423	423	100.00
2013(S)	415	411	99.04
2013(LS)	168	168	100.00
Total	**8811**	**7088**	**80.45**

Table 2.2: Annual number of database records with remarks (N) and proportion of individuals with wounds (PW) in adult female and adult male Painted Turtles (*Chrysemys picta*), Arowhon population, Algonquin Provincial Park. In 2013, "S" represents spring sampling (May and June) and "LS" presents late summer sampling (August and September). Odds ratio (OR) and 95% confidence intervals (95% CI) calculated as per Nakagawa and Cuthill (2007). Fisher's exact test significance values testing a difference in wound proportions between adult females and adult males, *<0.05, **<0.01, ***<0.005.

Year	**N_{female}**	**PW_{female}**	**N_{male}**	**PW_{male}**	**Odds ratio**	**Lower 95% CI**	**Upper 95% CI**
1990	103	0.06	23	0.13	0.41	0.095	1.79
1991	99	0.21	17	0.18	1.25	0.33	4.78
1992	135	0.17	24	0.04	4.69	0.61	36.76
1993	89	0.04	18	0.06	0.80	0.084	7.61
1994	96	0.22	19	0.00	***NA****		
1995	121	0.10	29	0.10	0.95	0.25	3.63
1996	133	0.05	30	0.03	1.37	0.16	11.82
1997	122	0.11	23	0.09	1.25	0.26	5.96
1998	194	0.13	46	0.07	2.11	0.61	7.35
1999	153	0.07	26	0.04	1.93	0.25	15.67
2000	170	0.12	32	0.00	***NA****		
2001	267	0.10	46	0.02	5.27	0.70	39.74
2002	320	0.15	71	0.03	**6.24*** **	**1.48**	**26.29**
2003	337	0.25	84	0.11	**2.81*** **	**1.35**	**5.86**
2004	350	0.20	96	0.13	1.78	0.92	3.44
2005	360	0.23	94	0.09	**3.12*** **	**1.45**	**6.71**
2006	324	0.23	79	0.10	**2.71****	**1.25**	**5.90**
2007	320	0.22	75	0.11	**2.34***	**1.08**	**5.11**
2008	334	0.13	74	0.04	**3.49***	**1.06**	**11.60**
2009	141	0.16	36	0.14	1.21	0.43	3.44
2010	256	0.14	54	0.06	2.69	0.80	9.10
2011	314	0.18	78	0.05	**4.10*** **	**1.44**	**11.68**
2012	309	0.18	78	0.09	2.25	0.98	5.14
2013(S)	305	0.44	64	0.22	**2.84*** **	**1.50**	**5.34**
2013(LS)	119	0.53	39	0.18	**5.14*** **	**2.10**	**12.57**
Mean (1990-2013S)		0.16		0.077	2.64		
95% CI		0.034		0.021	0.64		

Table 2.3: Proportion of wounds on eight body regions of Painted Turtles (*Chrysemys picta*) in the Arowhon population, Algonquin Provincial Park (1990-20130). Note that the summed proportions within a year may not total 1.00 due to rounding. In 2013, "S" represents spring sampling (May and June) and "LS" presents late summer sampling (August and September).

Year	Dorsal head, dorsal neck	Throat, ventral neck	Jawline	Lateral head and neck	Eyelid	Ambiguous, head or neck	Tail	Limb
1990	0.11	0.33	0.00	0.33	0.00	0.11	0.00	0.11
1991	0.52	0.00	0.11	0.15	0.00	0.00	0.07	0.15
1992	0.60	0.10	0.03	0.00	0.03	0.13	0.00	0.10
1993	0.00	0.17	0.17	0.00	0.00	0.00	0.67	0.00
1994	0.44	0.12	0.28	0.04	0.04	0.00	0.00	0.08
1995	0.40	0.20	0.20	0.07	0.00	0.07	0.07	0.00
1996	0.57	0.00	0.14	0.00	0.14	0.00	0.00	0.14
1997	0.31	0.50	0.00	0.06	0.00	0.00	0.00	0.13
1998	0.26	0.03	0.23	0.16	0.03	0.06	0.06	0.16
1999	0.43	0.21	0.00	0.29	0.00	0.00	0.00	0.07
2000	0.39	0.13	0.00	0.35	0.04	0.04	0.00	0.04
2001	0.19	0.13	0.13	0.03	0.03	0.28	0.00	0.22
2002	0.38	0.07	0.12	0.27	0.03	0.05	0.00	0.08
2003	0.29	0.33	0.10	0.12	0.03	0.07	0.01	0.06
2004	0.43	0.14	0.09	0.10	0.02	0.15	0.01	0.06
2005	0.43	0.21	0.11	0.13	0.01	0.08	0.00	0.02
2006	0.49	0.10	0.15	0.11	0.02	0.06	0.01	0.05
2007	0.38	0.15	0.18	0.10	0.00	0.12	0.01	0.06
2008	0.39	0.06	0.14	0.08	0.00	0.20	0.02	0.10
2009	0.34	0.17	0.20	0.09	0.03	0.09	0.06	0.03
2010	0.40	0.20	0.18	0.07	0.04	0.07	0.02	0.02
2011	0.31	0.39	0.14	0.06	0.03	0.00	0.01	0.06
2012	0.37	0.37	0.04	0.06	0.03	0.01	0.00	0.13
2013(S)	0.43	0.27	0.10	0.14	0.02	0.03	0.01	0.01
2013(LS)	0.21	0.49	0.08	0.16	0.03	0.00	0.01	0.03
Mean	0.36	0.19	0.12	0.12	0.02	0.07	0.04	0.08
SD	0.14	0.14	0.08	0.10	0.03	0.07	0.13	0.06
SE	0.03	0.03	0.02	0.02	0.01	0.01	0.03	0.01

Table 2.4: Quantification and comparative analysis of wounding between body locations for Painted Turtles (*Chrysemys picta*) in the Arowhon population, Algonquin Provincial Park (1990-2013(S)). Pairwise standardized effect size (Cohen's *d*) represents the difference in wounding between the body locations (Nakagawa and Cuthill 2007). When $d = 1$, the mean proportion of wounds between the locations differs by one standard deviation. A Kruskal-Wallis analysis tested the null hypothesis that there is no difference in mean wound proportions between body locations, $*p < 0.05$, $**p \leq 0.001$, $***p < 0.0001$.

Wound location	**Dorsal head, dorsal neck**	**Throat, ventral neck**	**Jawline**	**Lateral head and neck**	**Eyelid**	**Ambiguous, head or neck**	**Tail**	**Limb**
Nape, dorsal head								
Throat, ventral neck	**1.22*** **							
Jawline	**2.24*** **	0.70						
Lateral head and neck	**2.07*** **	0.63	0.02					
Eyelid	**3.46*** **	**1.70*** **	**1.62****	**1.32****				
Ambiguous, head or neck	**2.76*** **	**1.17***	0.71	0.63	0.75			
Tail	**2.39*** **	**1.12*** **	**0.70****	**0.66****	0.18	0.22		
Limb	**2.77*** **	**1.11***	0.61	0.53	**1.18***	0.18	**0.34*****	

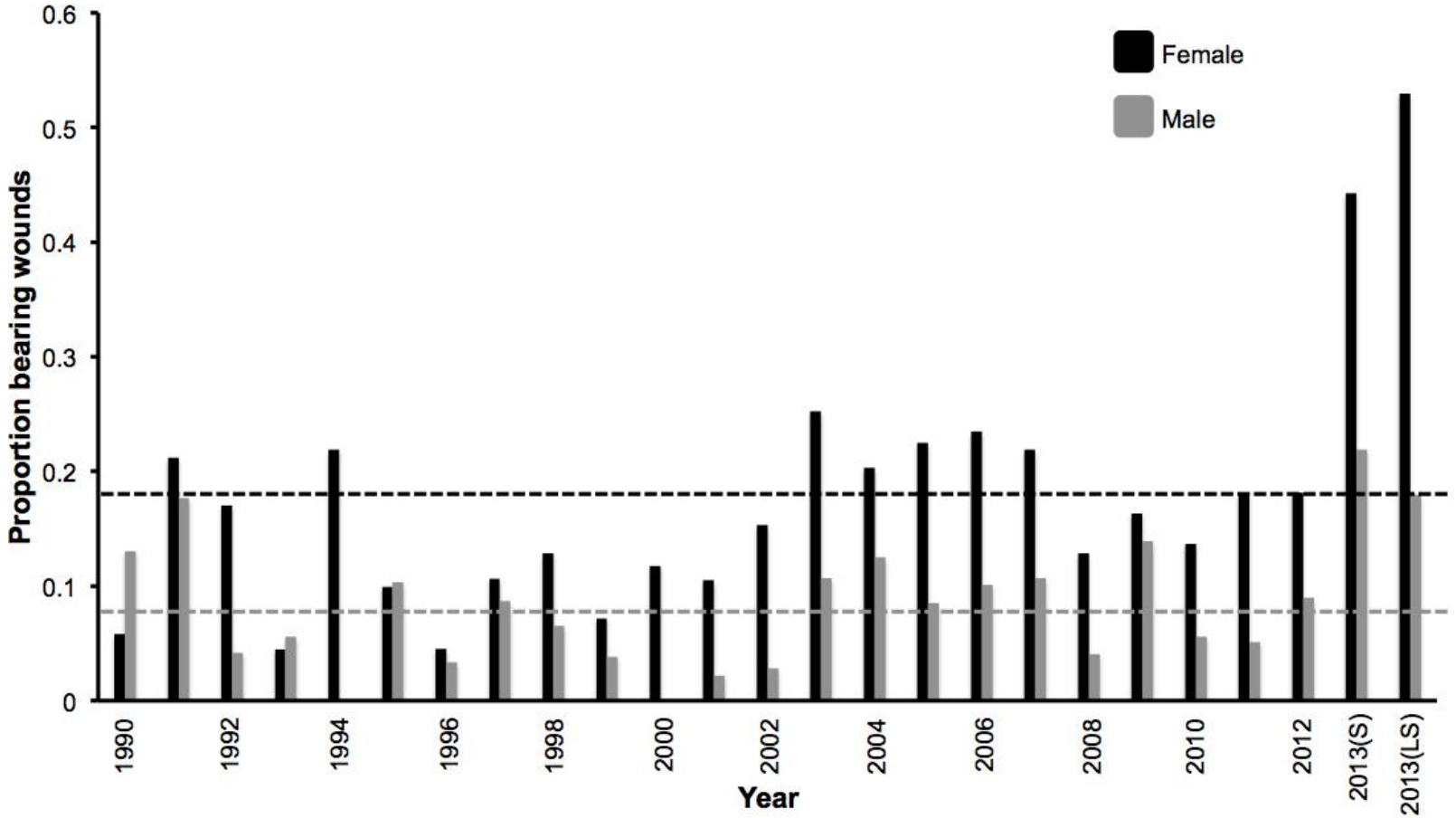

Figure 2.1: Wounding of adult female and male Painted Turtles (*Chrysemys picta*) in the Arowhon population, Algonquin Provincial Park (1990-2013). Dashed lines represent mean wound proportion across the 24-year dataset (1990-2013(S); female in black, male in gray). In 2013, "S" represents spring sampling (May and June) and "LS" presents late summer sampling (August and September)

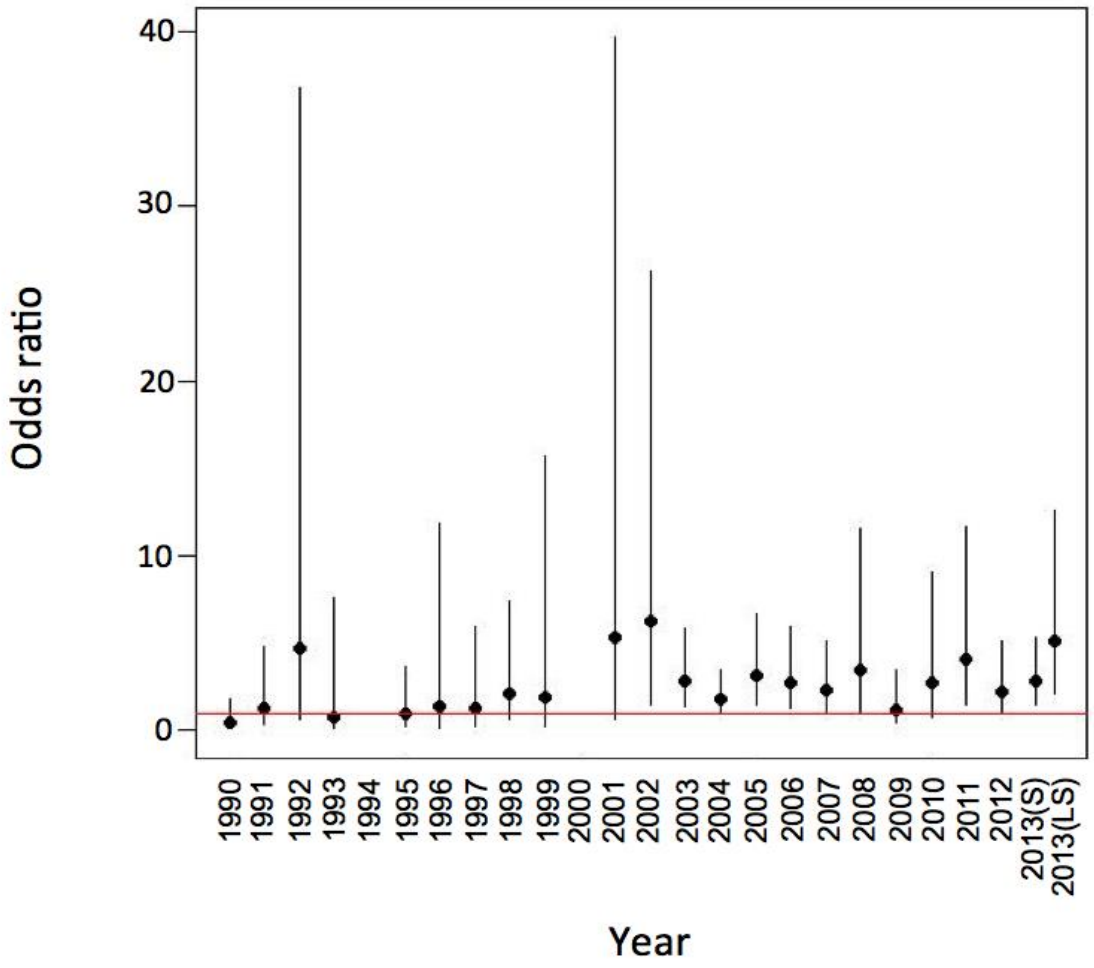

Figure 2.2: Female and male Painted Turtle (*Chrysemys picta*) wound odds ratios (±95% confidence interval) in the Arowhon population, Algonquin Provincial Park (1990-2013 spring and fall). Red line represents a 1:1 ratio of proportional female wounds:male wounds. When the odds ratio is >1, the proportion of female wounds exceeds that of males. Odds ratio could not be calculated in years when individuals of one sex (*i.e.*, male) did not demonstrate wounds (*i.e.*, 1994, 2000). The year 2013 is represented with 2013 spring (S) and 2013 late summer (LS) odds ratios.

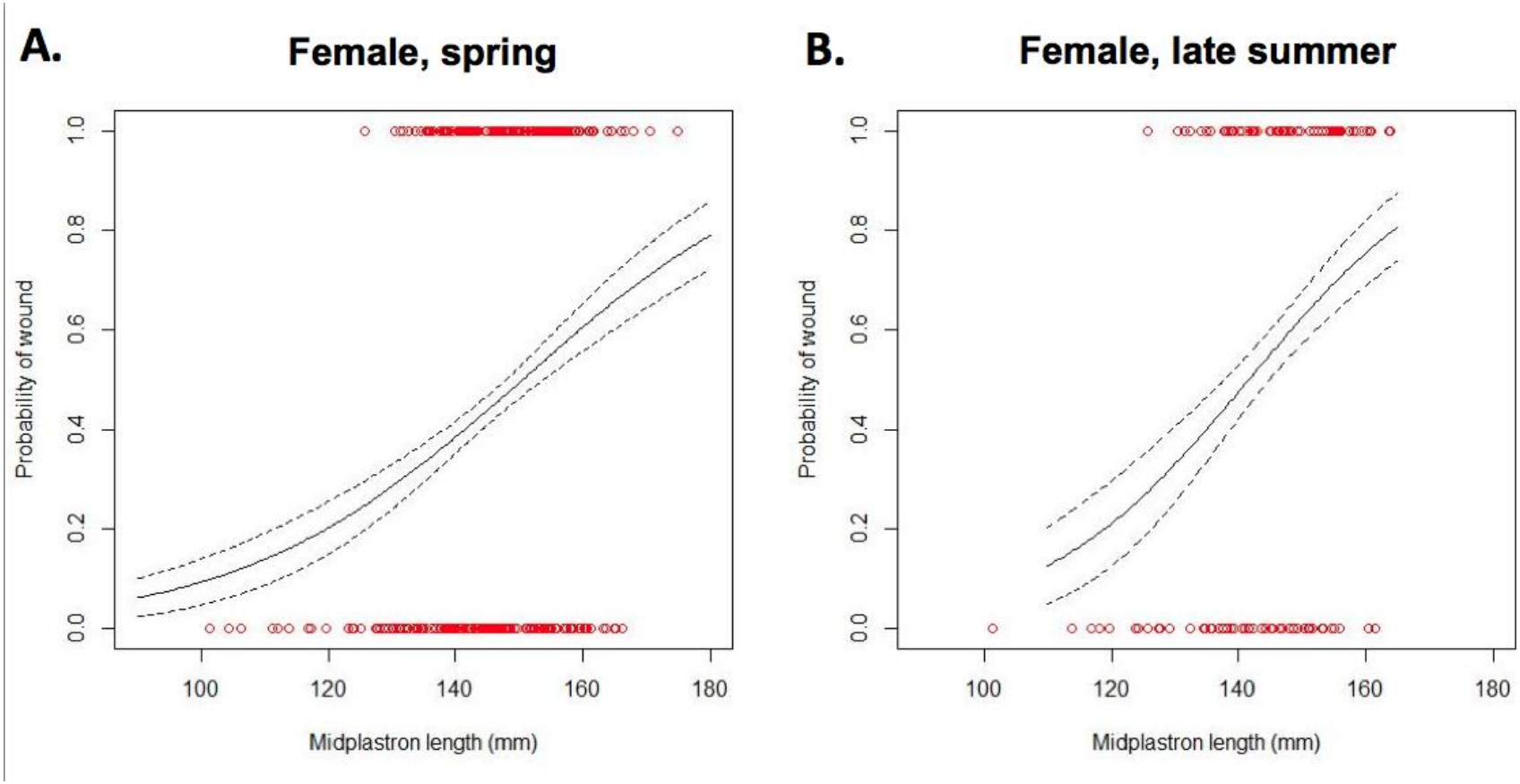

Figure 2.3: Probability of wounding by size in adult female Painted Turtles (*Chrysemys picta*), Arowhon population, Algonquin Provincial Park. A. Spring sampling 2013 (n = 305), B. Late summer sampling 2013 (n = 119). Female size at maturity in the Arowhon population is approximately 121.2 - 141.9 mm (average 13.0 mm, Samson 2003).

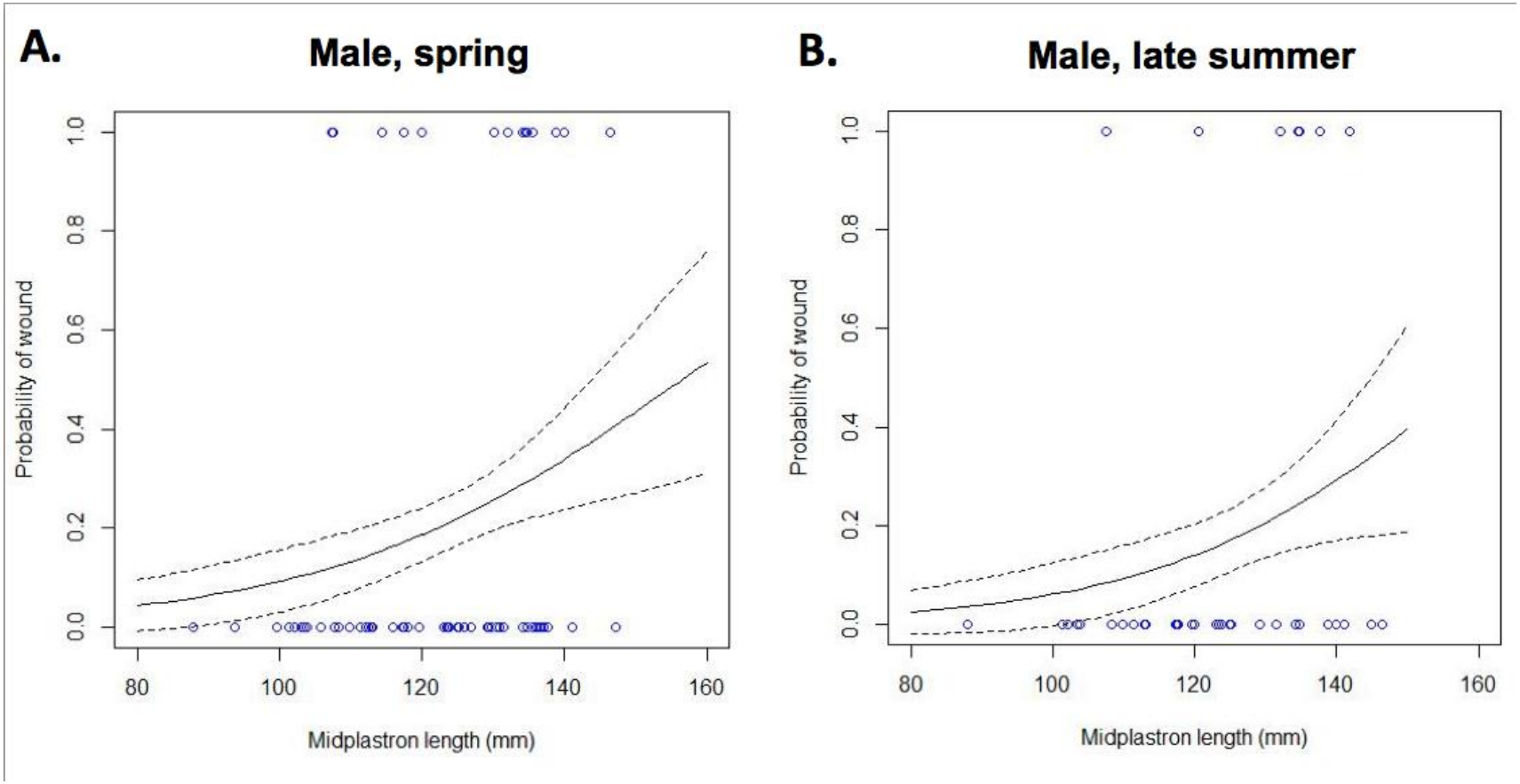

Figure 2.4: Probability of wounding by size in adult male Painted Turtles (*Chrysemys picta*), Arowhon population, Algonquin Provincial Park. A. Spring sampling 2013 (n = 64), B. Late summer sampling 2013 (n = 39). Male size at maturity in the Arowhon population is approximately 85.0 – 95.0 mm (Samson 2003).

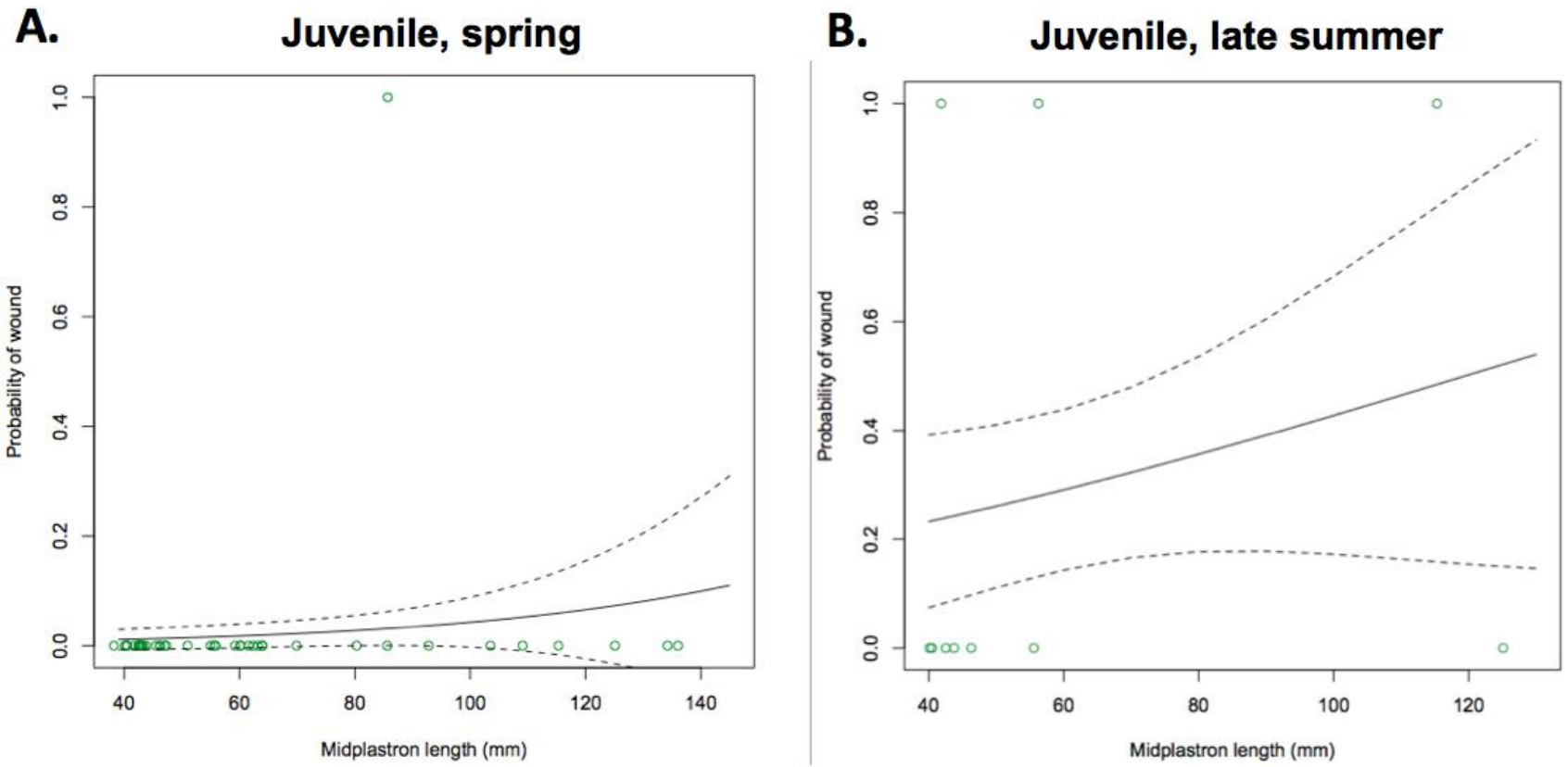

Figure 2.5: Probability of wounding by size in juvenile (unknown sex) Painted Turtles (*Chrysemys picta*), Arowhon population, Algonquin Provincial Park. A. Spring sampling 2013 ($n = 42$), B. Late summer sampling 2013 ($n = 10$). In the Arowhon population, female size at maturity is approximately 121.2 - 141.9 mm (average 13.0 mm) and male size at maturity is approximately 85.0 – 95.0 mm (Samson 2003).

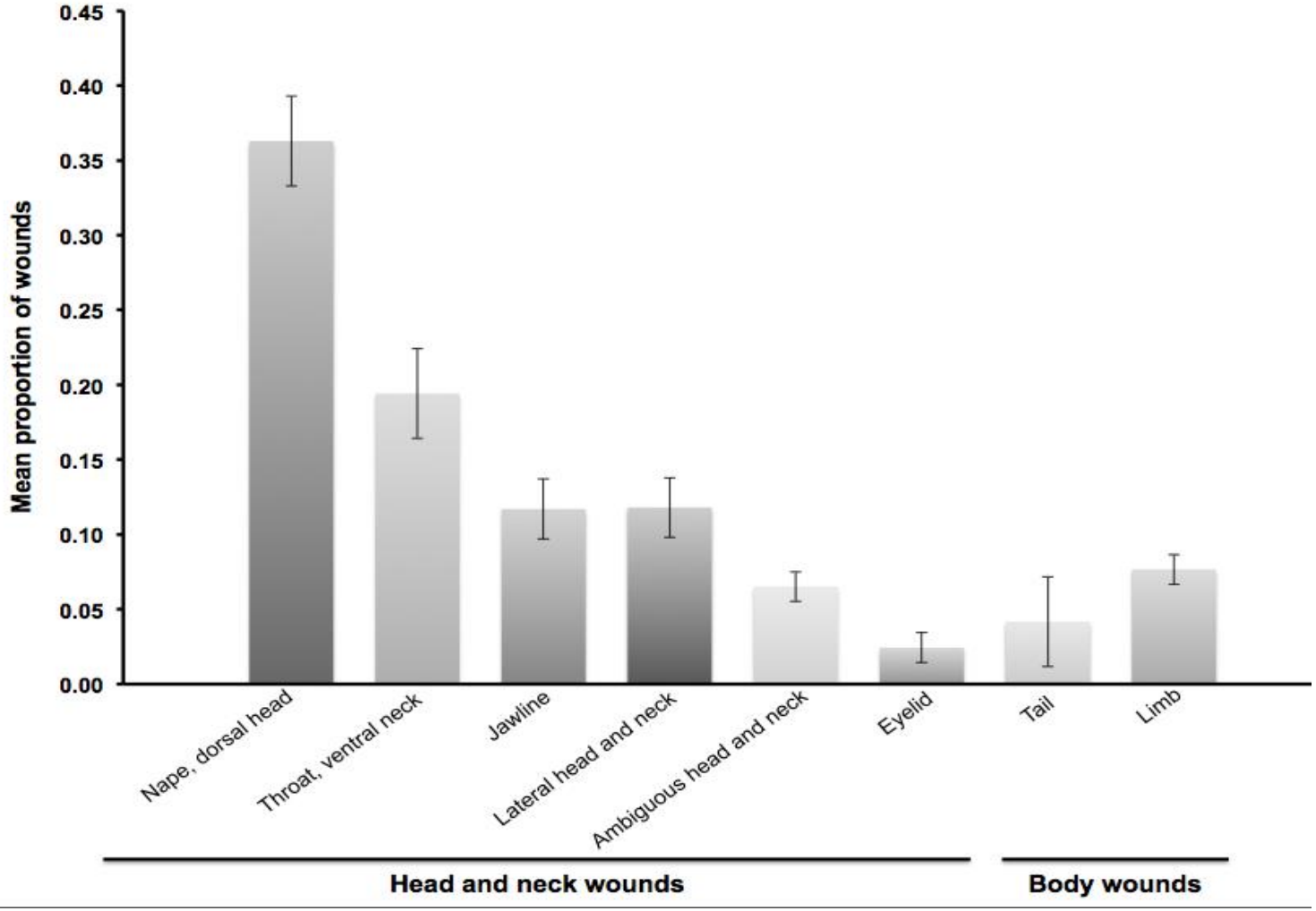

Figure 2.6: Proportional wounding observed across body regions on Painted Turtles (*Chrysemys picta*) in the Arowhon population, Algonquin Provincial Park, in spring 2013.

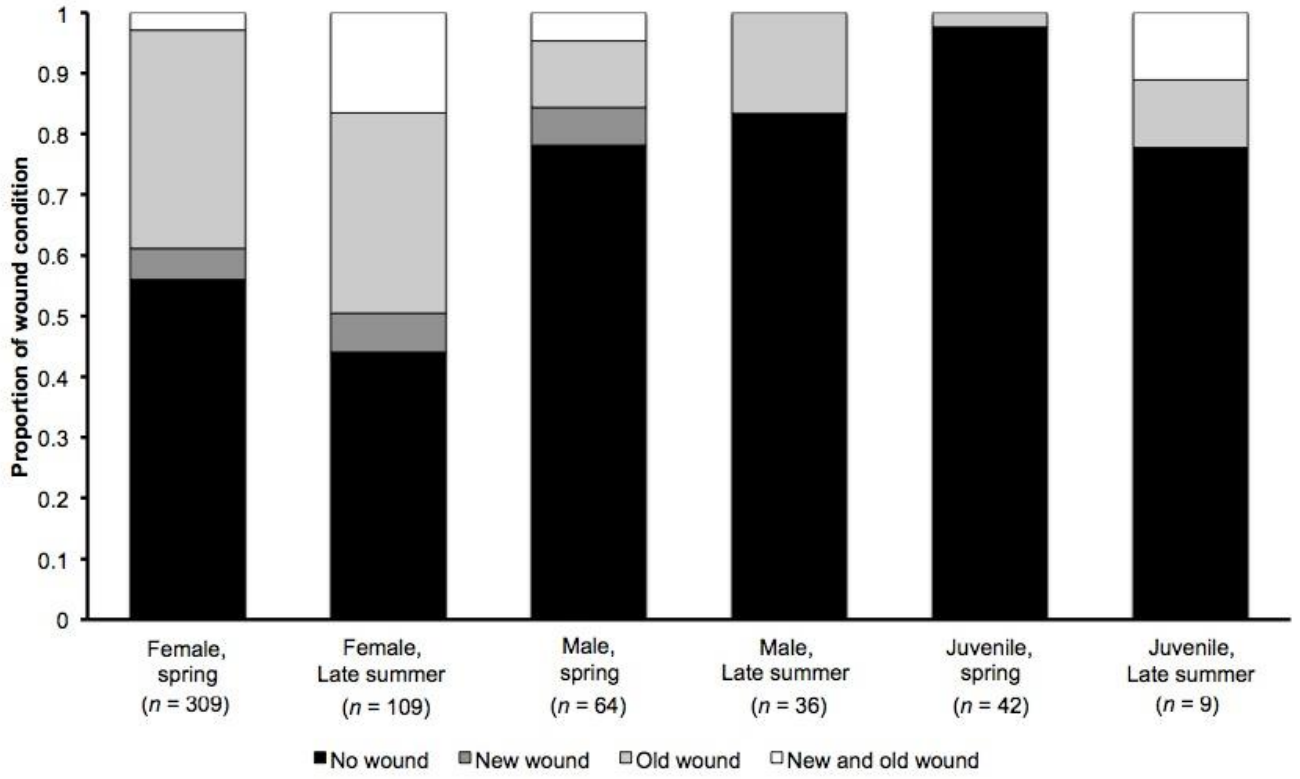

Figure 2.7: Wound condition (no wound, new wound, old wound, both new and old wound) across sex (juveniles of unknown sex, adult female, adult male) and season (spring, late summer) on Painted Turtles (*Chrysemys picta*) in the Arowhon population, Algonquin Provincial Park.

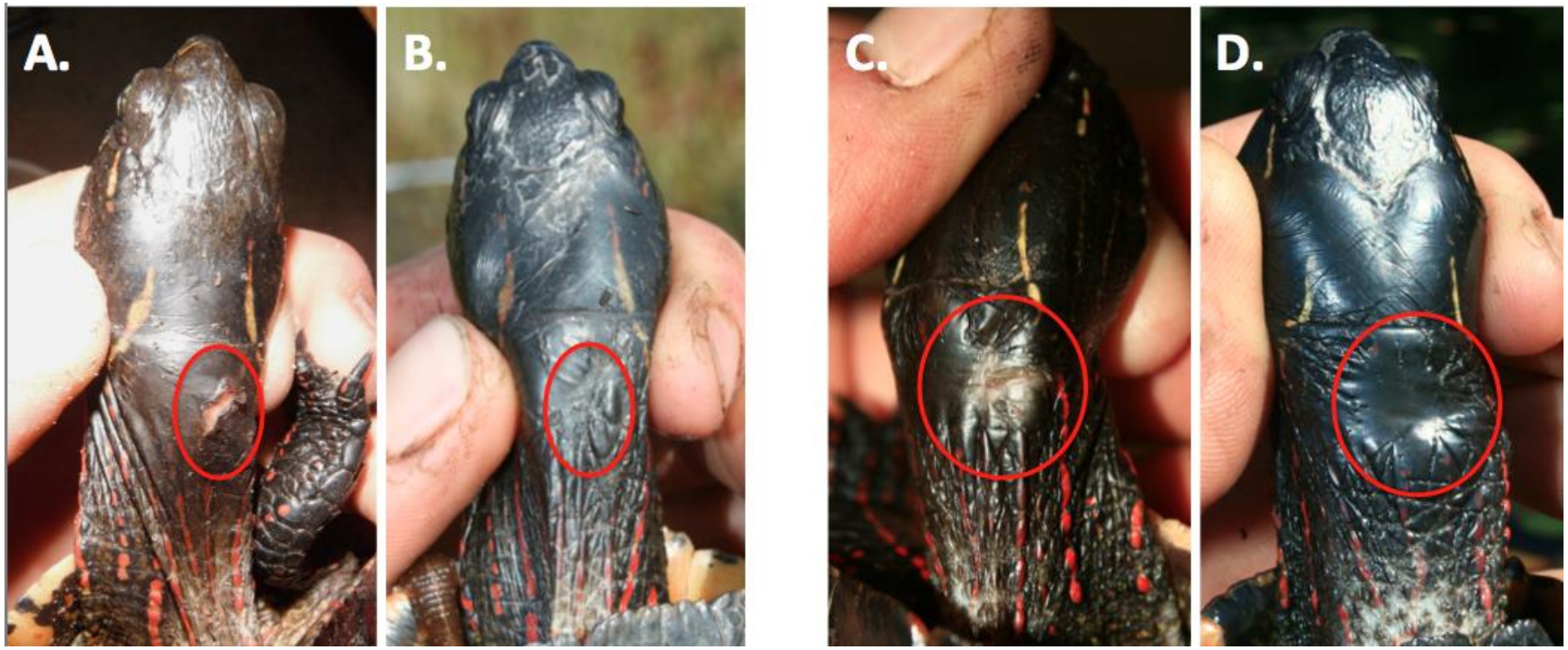

Figure 2.8: Female Painted Turtles (*Chrysemys picta*) from the Arowhon population, Algonquin Provincial Park, with observed wounds in the spring and subsequent recapture in the late summer of 2013. Painted Turtle ID 0215 on A) 9 June 2013 and B) 21 August 2013. Painted Turtle ID 0099 on C) 13 May 2013 and D) 29 August 2013.

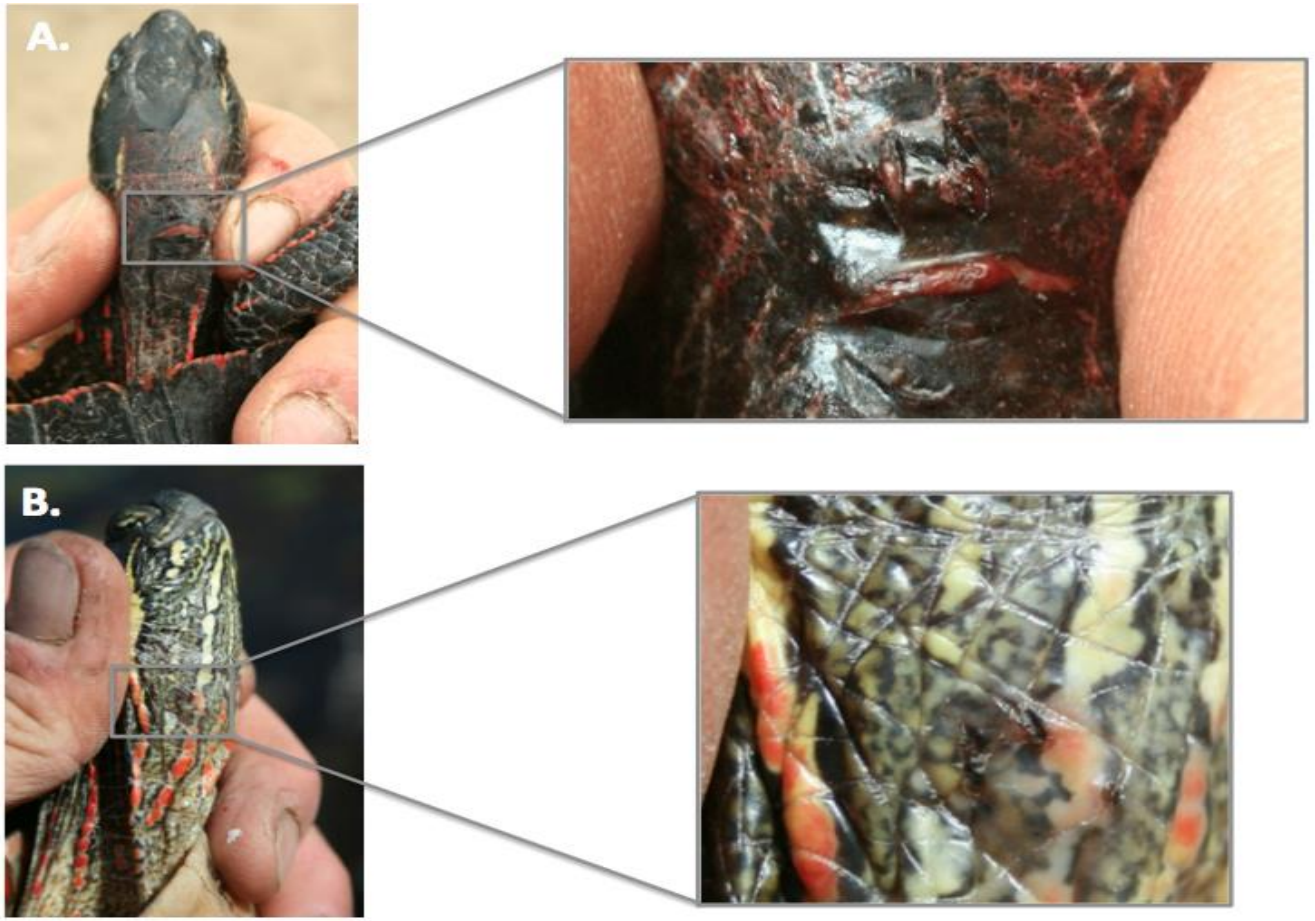

Figure 2.9: Female Painted Turtles (*Chrysemys picta*) from the Arowhon population, Algonquin Provincial Park, demonstrating fresh parallel gash marks that resemble tomiodont bite wounds. A. Painted Turtle ID 2787, 3 May 2013; B. Painted Turtle ID 0090, 6 September 2013. Also see Figure 2.10.

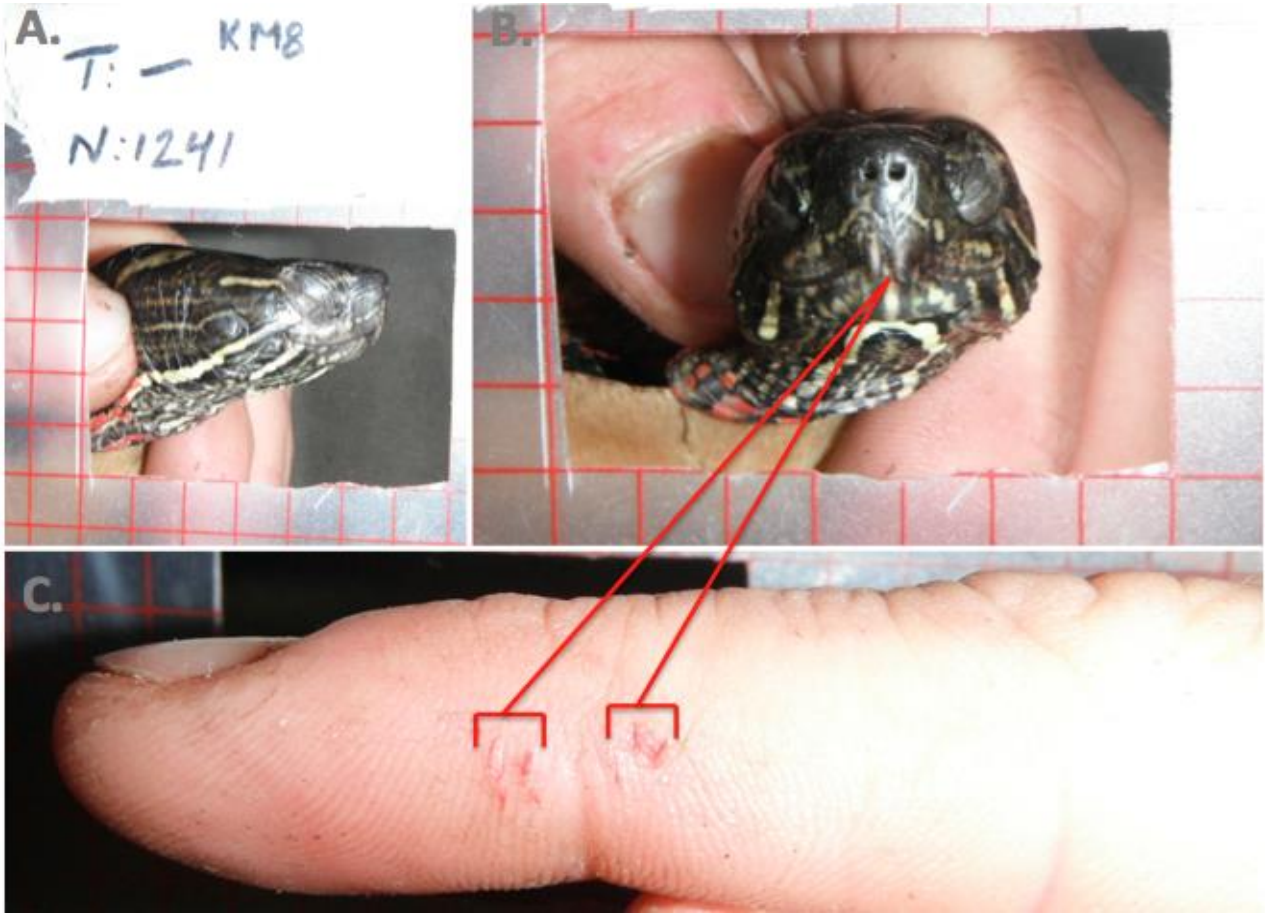

Figure 2.10: Bite wound from male Painted Turtle (*Chrysemys picta*) ID 1241. A) lateral head view of *C. picta* ID 1241, B) frontal head view, C) During processing *C. picta* ID 1241 bit the author (P. Moldowan) twice on the right index finger leaving two sets of parallel gashes, similar to those seen as fresh bite wounds of conspecifics (refer to Figure 2.9).

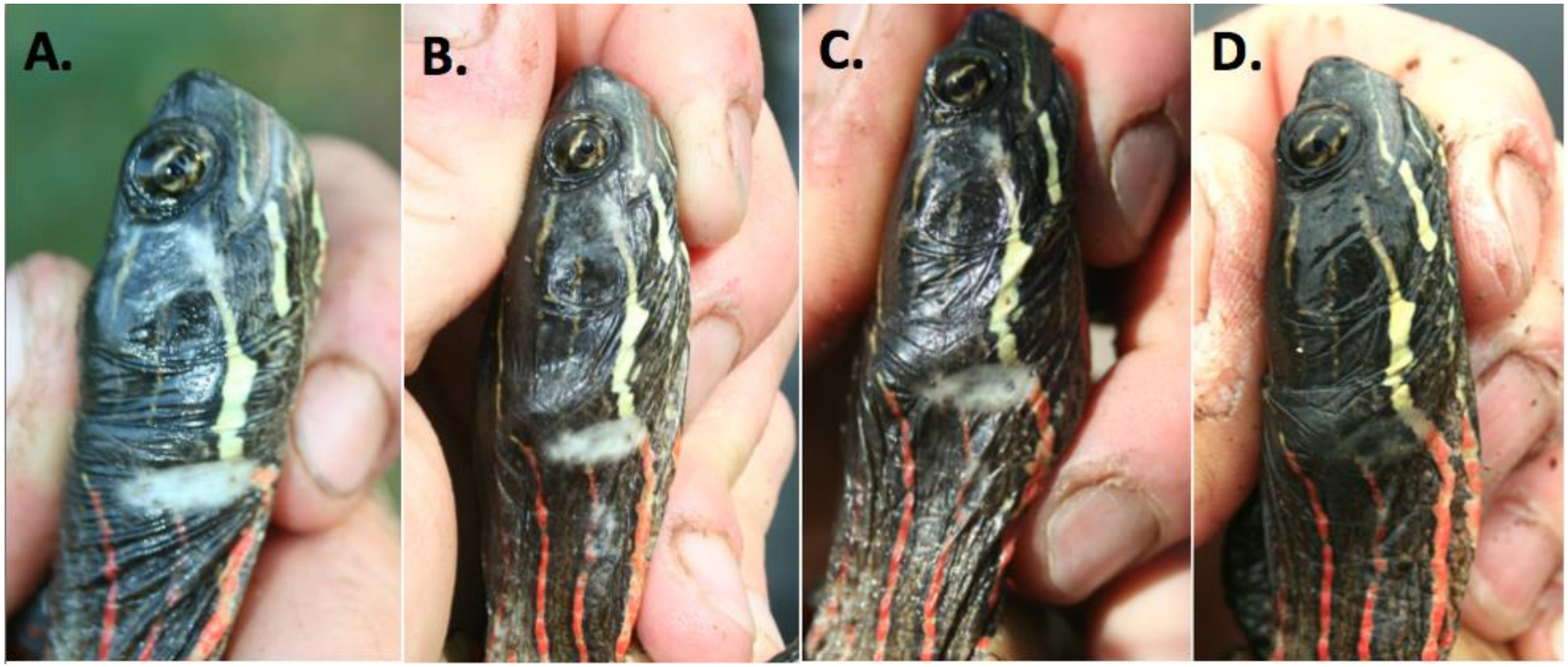

Figure 2.11: Right lateral head wound healing in wild female Painted Turtle (*Chrysemys picta*) ID 0051 from the Arowhon population, Algonquin Provincial Park. Late summer recaptures demonstrate, A) well-defined oval white scar, 21 August 2013. B) minimal change in wound condition, 27 August 2013. C) minimal darkening of scar tissue, 29 August 2013. D) subtle white scarring remains, re-melanisation has reduced oval scar to two conjoined white circular ring scars, 20 September 2013.

Figure 2.12: Dorsal head wound healing in wild female Painted Turtle (*Chrysemys picta*) ID 0051 from the Arowhon population, Algonquin Provincial Park. Painted turtle ID 0051 was captured 14 August 2013 with no dorsal head wound. Late summer recaptures demonstrate, A) fresh wound with small patch of dried fresh blood anteriorly, 17 August 2013. B) Very early wound scabbing and discolouration, blood vessels observed near surface of wound, 21 August 2013. C) Continued wound scabbing, 27 August 2013. D) Scab recession revealing underlying white scarring, 29 August 2013. E) Late scar healing and re-melanisation of tissue, 20 September 2013.

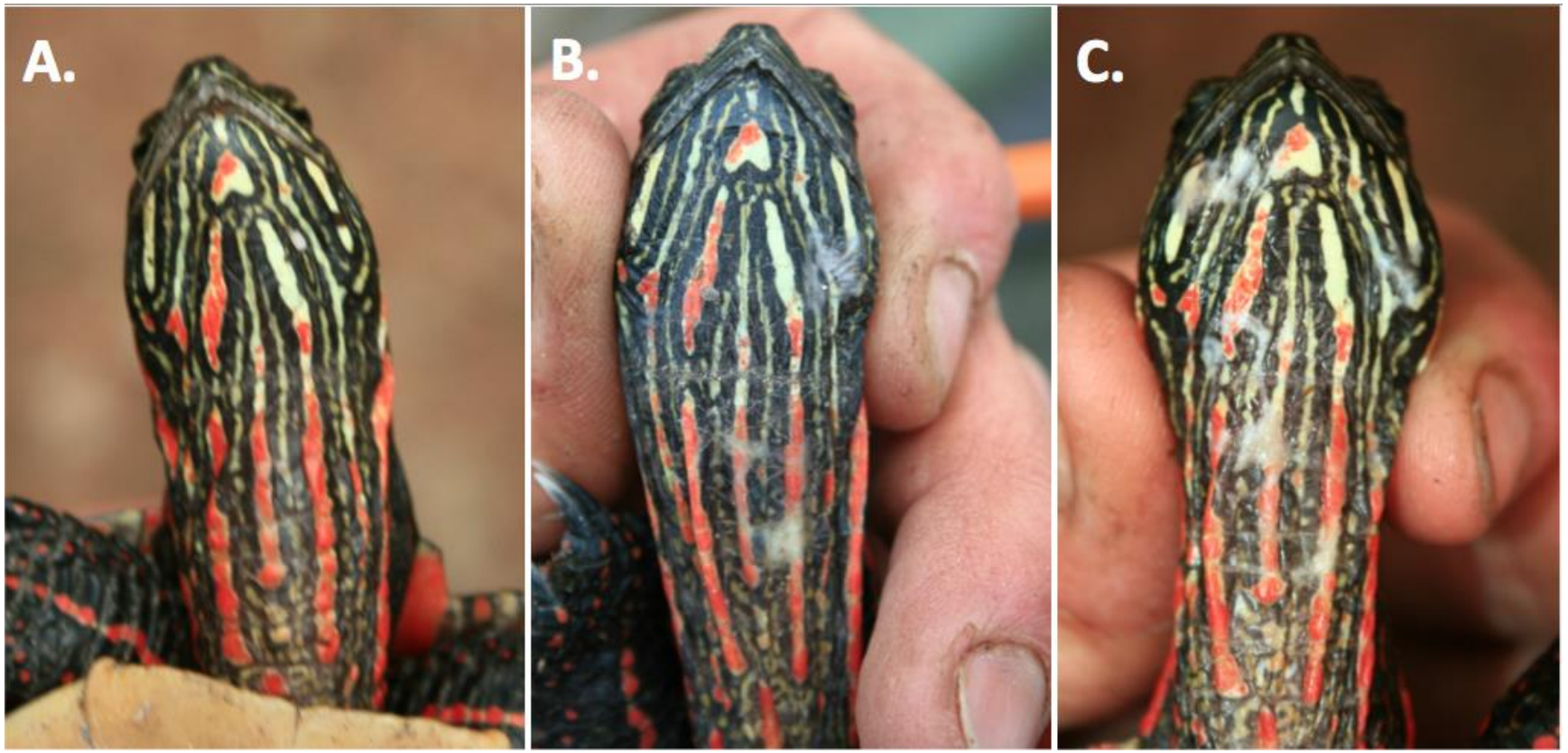

Figure 2.13: Wounding condition on the throat and ventral neck of female Painted Turtle (*Chrysemys picta*) ID C48 tag, 0750 notch in the spring and late summer of 2013 and spring of 2014. A) No wound observed, 8 May 2013; B) white patchy scarring on throat near posterior left lower jaw and centre on ventral neck, 14 August 2013; C) white patchy scarring on throat and ventral neck, including unhealed scars from the late summer of 2013, 21 May 2014.

Chapter III

Courtship or coercion?
Alternative reproductive tactics in the
Midland Painted Turtle
(*Chrysemys picta marginata*)

"*Males are significantly smaller than females so, rather than try to overpower the females as the larger male Snapping and Wood Turtles do, the Painted Turtle shows a much more decorous approach, pursuing the female, getting in front of her, then stroking her face and neck with his elongate foreclaws … the above description of mating is one that people like as it emphasizes a gentle lifestyle … however, over the past several years, researchers in Algonquin noticed that female Painted Turtles often have fresh wounds and scars on their face and neck, something one never sees on female Snapping Turtles. Observations of mating behaviour in turtles are difficult in the wild, because mating takes place in water and the boggy waters of the Park are so tea-coloured that turtles are almost impossible to discern underwater. Nevertheless, we have enough observations to indicate that the facial wounds on females are inflicted by male suitors who have been rejected. Males bite the reluctant female and often won't let go even when she retracts her head into the shell. It is tempting to explain this behaviour of the male as spiteful, but we really have no idea why it occurs, why it is so common, or why the larger female puts up with it. Regardless, the contrast between what we expect and what we find after careful study is often remarkable*."

R.J. Brooks, D. Strickland, and R.J. Rutter
Reptiles and Amphibians of Algonquin Provincial Park (2000)

"*Most progress in sexual selection theory has been made in animal models that are easy to observe in nature such as fish, lizards, and birds … Less is known about the behaviour and social systems of freshwater turtles because they often live in turbid water, making direct observations difficult. Instead, speculation often prevails … The behaviour of freshwater turtles is likely to be interesting, but advancing our knowledge in this area will likely require carefully designed experiments rather than anecdotal observations coupled with speculation*."

Hites *et al*. 2014
Herpetological Review 44(1): 46-49.

"*Titillation's been replaced.*"

Gord Downie, The Tragically Hip
"Vapour Trails", Phantom Power (1998)

Chapter III: Courtship or coercion? Alternative reproductive tactics in the Midland Painted Turtle (*Chrysemys picta marginata*)

Abstract: The mating tactics of the Painted Turtle (*Chrysemys picta*) are well-recognized as involving an elaborate male courtship display coupled with female mate choice. Traditionally it is thought that female *C. picta* choose mates on the basis of courtship display and/or traits that demonstrate male quality. *In situ* field observations and experimental trials from a long-term study of *C. picta* in Algonquin Provincial Park (Ontario, Canada) suggest that males also demonstrate alternative, coercive mating tactics. Males are equipped with prominent tomiodonts, tooth-like cusps of the upper jaw, which seemingly function in immobilizing mates and result in extensive wounding to the head and neck of females. Over 100 hours of video recordings from experimental trials during the spring and fall (2013) breeding periods showed that small males court females through titillation, whereas larger males employ coercive tactics, such as striking, biting, and forced submergence. Late summer, rather than spring, appears to be the primary breeding season of Arowhon population *C. picta* in Algonquin Provincial Park. I report a novel shell clattering behaviour in *C. picta*, only the second species of chelonian in which this behaviour has been described. My findings are contrary to the female choice mating system reported for *C. picta* and join a growing body of recent research demonstrating the importance of coercive tactics in the reproduction of male emydid turtles. I propose that male *C. picta* exhibit sexual weapons in the form of tomiodonts used in mate coercion and challenge the notion that sexual coercion is unlikely in open-water and free-swimming freshwater turtles.

Introduction

Sexual selection and coercion

Research on sexual selection has largely focused on mate choice, male-male contests, and sperm competition, although many alternative mechanisms exist, such as scramble competition, and notably, sexual coercion (Andersson 1994, Andersson and Iwasa 1996). Sexual coercion is defined as the use of force, or threat of force, by a male to increase his chances that a female will mate during a fertile period and decrease the chances that she will mate with other males (Smuts and Smuts 1993, Andersson and Iwasa 1996). Females incur a cost from the sexually coercive behaviours of males (Smuts and Smuts 1993). Multiple forms of sexual coercion have been described: (1) forced copulation, during which a male physically restrains a female while achieving copulation

by force; (2) harassment, when males make repeated attempts to copulate with females who are coaxed into mating to costs created by harassment; and (3) intimidation, when males punish females that resist copulation, in turn increasing the chances that a female will be accepting of future mating attempts (Clutton-Brock and Parker 1995, Andersson and Iwasa 1996). These mechanisms of sexual selection are not necessarily mutually exclusive and may co-occur in a species or population (Smuts and Smuts 1993, Bisazza *et al*. 2001).

Reproductive tactics can be highly dynamic, condition- and context-dependent. For instance, male guppies (*Poecilia reticulata*) shift mating tactics from courtship to coercion in response to female behaviour and to reduce predation risk (Magurran and Nowak 1991). Despite sexual coercion being the dominant mating tactic of male mosquitofish (*Gambusia holbrooki)*, females are still capable of some mate choice, demonstrating that these two tactics can coexist (Bisazza *et al*. 2001). Female garter snakes (*Thamnophis sirtalis*) experience cryptic coercion whereby males exploit features of female respiratory anatomy, physiology, and antipredatory behaviour to accomplish forced insemination (Shine *et al*. 2005). Slider turtles (*Trachemys scripta*) and Cooters (*Pseudemys nelsoni*) undergo an ontogenetic shift in mating tactics whereby young males demonstrate pre-copulatory courtship displays whereas older males adopt coercive behaviours, such as chasing and biting (Kramer 1986, Thomas 2002). Compared to intrasexual competition (often between males) and mate choice (often by females), sexual coercion (often male coercion of females) is not widely recognized as an alternative form of sexual selection (Smuts and Smuts 1993). However, a growing number of examples of sexual coercion suggest that it is an important male reproductive tactic.

Sexual conflict and male-female sexual antagonism

Males and females have divergent reproductive interests arising from the unequal (and often female-biased) investment in offspring (Trivers 1972, Andersson 1994). The reproductive potential of a female is limited by her ability to reduce costs associated with mating and to invest energy and time into offspring (Andersson 1994, Rowe 1994, Rowe *et al*. 1994, Andersson and Iwasa 1996). In contrast, males may invest relatively little into reproduction and incur relatively low mating costs compared to females, yet males can achieve high reproductive potential by mating with multiple females (Gavrilets *et al*. 2001, Chapman *et al*. 2003). Reproductive events, such as mating frequency, fertilization, relative parental effort, number of partners, female reproductive rate, and clutch size, are points of conflict between the sexes (Gavrilets *et al*. 2001, Chapman *et al*. 2003). Each sex is expected to participate in reproduction with its own interests foremost. This sexual conflict can result in an antagonistic coevolutionary arms race through sexual selection (Dawkins and Krebs 1979, Parker 1979, Clutton-Brock and Parker 1995, Arnqvist and Rowe 2002) whereby each sex strives to maximize their reproductive potential while attempting to minimize the reproductive costs associated with mating, parental investment, and offspring care. As a result of competing interests, both sexes are expected to evolve sexually antagonistic adaptations that influence reproductive outcomes in their favour (Rice 1998, Chapman *et al*. 2003). Male traits can be subject to sexual selection as females develop preferences for traits in partners and become increasingly choosy in an attempt to optimize their reproductive interests and fitness (Arak and Enquist 1993, Andersson 1994). Females may also seek indirect genetic benefits for their offspring by mating with preferred males (Fisher 1958). Female mating

resistance and mate choosiness would thus promote male display traits that exploit female preferences and/or alternative male reproductive tactics. Genetic studies suggest that male traits and behaviours are subject to antagonistic coevolution and can become exaggerated from sexual conflict (Rice 1992, Gavrilets *et al*. 2001, Gibson 2002). Given that males generally invest less in reproduction than females (*e.g*., lower initial investment in gamete production, parental care, *etc*.; Trivers 1972), we expect that females impose selection for traits that increase reproductive provisioning from males, in turn reducing the reproductive burden on females. This reproductive cost-sharing can impart selection on male display traits, courtship demonstrations, nuptial gifts, and parental care. However, in the sexual antagonism arms race, males are expected to resist such costly investments and may do so by adopting alternative reproductive tactics.

Alternative reproductive tactics

Alternative reproductive tactics refer to two or more (*alternative*) ways to obtain fertilizations in both males and females (Taborsky *et al*. 2008). Intrasexual and intraspecific competition impose selection to maximize reproductive fitness through alternative reproductive tactics (Gross 1996, Taborsky *et al*. 2008). The traits that form the basis of alternative reproductive tactics, whether morphological (*e.g*., size dimorphism, dimorphic structures) or behavioural (*e.g*., courting vs. sneaking), must have a dichotomous distribution and individuals must allocate resources to one alternative or the other at a given time to achieve the same functional end result, reproduction in this case (Brockmann 2001, Taborsky *et al*. 2008). The distinction between reproductive tactic and strategy (Dominey 1984, Gross 1996) is not made here and the two terms are

treated synonymously (see discussion by Taborsky *et al*. 2008).

Competing reproductive tactics are expected to result in exaggeration of sexually selected characters (*e.g*., sexual dimorphism in body size), and development of weapons, and/or costly ornaments (Neff 2001). These dimorphic traits are often found in conjunction with complementary behaviours. For example, male body size and the presence of horns in the dung beetle (*Onthophagus* spp.) are related to a fighting vs. non-fighting tactics during mating (Kotiaho and Tomkins 2001). Alternative reproductive tactics within an individual or population shift in response to fitness optima, varying with ontogeny, social ranking (*e.g*., dominant vs. subordinate), physical condition, and local environmental conditions (*e.g*., competitors, density, sex ratio, resource availability) (Rowe *et al*. 1994, Halliday and Tejedo 1995, Gross 1996, Alonzo *et al*. 2000, West-Eberhard 2003, Westneat and Stewart 2003, Taborsky *et al*. 2008).

Sexual conflict in the Painted Turtle (*Chrysemys picta*)

Female turtles invest more into reproduction than males, as is the case with most animals (Trivers 1972). In female Painted Turtles, reproductive effort (including courtship, mating, egg production, and nesting) has been estimated to require 48% of the annual energy budget, with egg production alone accounting for 14% of the total (Congdon *et al*. 1982). Mate searching and courtship are purported to be energetically expensive in male emydids (Jackson and David 1972, Kramer 1989, Kramer and Burghardt 1998, Pearse *et al*. 2002), although this remains to be quantified. Furthermore, males have higher reproductive variation than females. Male *C. picta* may sire offspring

from multiple clutches with multiple females in a single reproductive season (Pearse and Avise 2002, Pearse *et al*. 2002, McTaggart 2000, Ernst and Lovich 2009, Hughes 2011). Reproductive investment by male *C*. *picta* is seemingly limited to pre-copulatory courtship display and sperm production. Parental care is absent in the species.

Reproductive tactics and reports of male-female antagonism in Chrysemys picta

Painted Turtle reproductive tactics have been described as male courtship with female mate choice (Ernst 1971*a*, Berry and Shine 1980, McTaggart 2000, Ernst and Lovich 2009). During breeding, males actively participate in a courtship display known as titillation, involving stroking the female with the lengthy claws of the forefeet (Taylor 1933, Cagle 1954, Ernst 1971*a*, Ernst and Lovich 2009). Receptive females may return titillation behaviours or sink to the substrate, which is followed by male mounting and copulation (Taylor 1933, Ernst 1971*a*, Ernst and Lovich 2009). It is thought that female *C*. *picta* select mates on the basis of courtship display and/or traits that demonstrate male quality (Berry and Shine 1980, McTaggart 2001, Hughes 2011). However, male courtship may not be the only reproductive tactic of Painted Turtles.

Gibbons (1968*a*) reports two observations during the spring reproductive period of males biting the plastron of a female and attempting to restrain her. From the captive husbandry and propagation of *C*. *p*. *dorsalis*, Roddewig (2014) noted contrasting male reproductive behaviours: one male would actively chase females and preferentially bite their neck (or occasionally the leg or tail) during courtship, whereas another male would only engage in a titillation display. Liu *et al*. (2013) state that biting is part of the *C*. *picta* reproductive behavioural repertoire, but provide little supporting evidence. Field observations of male-female antagonism have been observed in the long-term Arowhon

study population of *C. p. marginata* in Algonquin Provincial Park, Ontario (Appendix V). Researchers have recorded *in situ* male biting, female resistance, and soft tissue injuries principally found on the head and neck of females (Chapter II, also see Appendix V). Such observations beg numerous questions about the significance of male aggression and its possible role in the mating tactics of *C. picta*.

Research direction

There has been a longstanding appeal for published observations of chelonian reproductive behaviour (Carpenter and Ferguson 1977, Harless 1979, Berry and Shine 1980, Lui *et al*. 2013). Reports on chelonian reproductive behaviour are often anecdotal, limited to a single species, and lack the scope (*e.g*., replication, multiple breeding animals) necessary for rigorous hypothesis testing. As such, Lui *et al*. (2013) provide recommendations for future research, including the collection and publication of natural history data, hypothesis testing, and the standardization of terminology in the study of chelonian reproductive biology and courtship. My study satisfies all three of the abovementioned criteria in an attempt to describe and experimentally examine the reproductive behaviour of *C. picta*.

Even as one of the most well-studied turtles in North America (Lovich and Ennen 2013), and arguably the world, the reproductive behaviour in *C. picta* is still poorly understood. The objective of the work presented in Chapter III was to conduct behavioural trials to assess courtship and pre-copulatory behaviour in *C. picta,* testing for biting and use of tomiodonts as part of a coercive mating tactic. I have presented multiple lines of evidence to suggest that coercive mating tactics are present in the Arowhon *C.*

picta population, Algonquin Provincial Park: male-biased tomiodont dimorphism (Chapter I), female-biased soft tissue wounding occurring primarily during the reproductive season (Chapter II), and sporadic field observations of male-female antagonism (Appendix V). More rigorous visual confirmation is necessary to unite the former two observations and substantiate their relationship (if any) with coercive male behaviour. If the tomiodonts of male *C. picta* are related to reproductive success, then I would expect that males will employ the tomiodonts in coercive reproductive tactics. In Chapter III, I present an ethological evaluation of male *C. picta* reproductive behaviour from experimental behavioural trials during the spring and late summer breeding seasons. I again address the functional significance of the tomiodonts with the support of data from the behavioural trials. I also describe a novel shell clattering behaviour in *C. picta*, which appears to be more widespread across emydid taxa than presently recognized. Further, I explore the biological explanations for the occurrence of two putative reproductive tactics (*i.e.*, courtship and coercion).

Methods

Study population and site

The Arowhon study population of *C. picta* is located at three closely located ponds, Wolf Howl Pond, Wolf Howl Pond East, and West Rose Lake (45°34'N, 78°41'W), Algonquin Provincial Park, Ontario, where monitoring of population demographics and reproduction has taken place annually since 1978 (R.J. Brooks). Population estimates based on mark-recapture study approximate 400 adults at the three sites combined (Samson 2003). The Painted Turtles at the Arowhon sites are found at

variable population densities: Wolf Howl Pond ~ 128.6 turtles/ha, Wolf Howl Pond East ~ 17.9 turtles/ha, West Rose Lake ~16.3 turtles/ha (S. Sanders and M. Keevil, unpublished data). The sex ratio of the adult population is strongly female biased (3.44:1, female:male) (Samson 2003). A complete site description can be found in Schwarzkopf and Brooks (1985).

Behavioural trials

Behavioural trials were conducted in spring (14-31 May 2014) and late summer (15 August through 22 September 2014) during the two putative breeding periods of *C. picta* (Gibbons 1968*a*, Moll 1973, Krawchuk and Brooks 1998, Ernst and Lovich 2009). The onset of breeding is associated with temperature in *C. picta*. Mating occurs at water temperatures between 15.5°C and 21.2°C (Ernst 1971*a*). Basking temperatures greater than 17°C are required for the initiation of testis growth, spermatogenesis and testosterone secretion (Ganzhorn and Licht 1983, Licht and Porter 1985). Similarly, maximum ovarian growth and ovulation in female *C. picta* is achieved at 17°C (Ganzhorn and Licht 1983). Thus, spring behavioural trials commenced once the body temperature of recently captured basking turtles was ≥ 17°C and surface water temperature reached 15°C.

Turtles were captured by canoe and landing net from Wolf Howl Pond and Wolf Howl Pond East for behavioural trials. All individuals were marked members of the long-term study. Turtles had unique identification codes painted on their carapaces from capture earlier in the season when weighing and measurement took place. Males were maintained individually and separated from females (in open top buckets), whereas

females were permitted to interact between time of capture and being placed in a trial. Handling time was minimized and often did not exceed 10-15 minutes from time of capture to placement in a trial. One male and three females were placed in each trial, approximating the sex ratio in the Arowhon population (3.44:1, female:male; Samson 2003). Turtles were haphazardly assigned to a trial, although a conscious effort was made to vary female size in each trial. Within each breeding season, a male and female were only run once through one complete trial.

Enclosures (183 cm long x 76 cm wide x 76 cm deep; adapted from Exo-Terra® Flexarium, full screen terrarium, Rolf C. Hagen Inc., Montreal) were set-up partially submerged (water depth ~ 60 cm) in Wolf Howl Pond East (Figure 3.1). The enclosures were constructed of a lightweight PVC frame and fitted nylon mesh walls with an open top, thus permitting water flow and exposure to environmental stimuli (*e.g.*, light, olfactory cues) from the turtles' local habitat. Floatation devices were placed at each corner to elevate the upper frame of the enclosure out of the water and prevent turtle escape. A GoPro® camera was pole-mounted mid-way along the length of the enclosure and oriented to provide an overhead view of the trial. Trials were two hours in length beginning after the addition of all four turtles into the enclosure. Researchers were not present during the trials. Due to limitations in camera battery life no acclimation period was provided following the introduction of turtles into the trial (*i.e.*, recording and evaluation began immediately). Trials were conducted on clear days with low wind between the hours of 1000 and 1600 to maximize visibility. A total of 18 complete male-female spring trials (2 hours/trial; 36 hours) and 28 complete male-female late summer trials were recorded (56 hours). In addition, one all-female trial (four females in trial; 2

hours) and four all–male trials (four males in trial; 8 hours) were conducted in the late summer to evaluate intrasexual interactions during a breeding period. Incomplete trials (< 2 hours) were excluded from analysis (n = 2 trials from each the spring and late summer), unless specified otherwise.

Ethogram development and behavioural trial review

An ethogram was developed to describe and quantify the reproductive behaviours of *C*. *picta* recorded in the behavioural trials (Appendix VI). The ethogram was largely developed from the work of Jackson and Davis (1972), Baker and Gillingham (1983), Kramer (1984, 1986, 1989*a*,*b*), Thomas (2002), Pandav *et al*. (2007), and Davis (2009). Videos were reviewed and scored using the ethogram (Appendix VI). The reproductive behaviours of male C. *picta* were grouped into three different contexts including neutral interactions (approach, cloacal sniffing), courtship (titillation), and coercion (striking, biting, forced submergence, shell clattering) (Appendix VI). Recall that sexual coercion involves aggressive male behaviour toward females, including the use or threat of force and a resultant cost to the female (Smuts and Smuts 1993). In contrast, courtship is defined here as non-aggressive male reproductive behaviour directed toward a female with no apparent cost to the female. The time and recipient of a male's behaviour was recorded in video review. Behaviours resulting from two or more turtles accidentally bumping into each other while in an enclosure corner or swimming along the enclosure walls were excluded from analysis (Thomas 2002).

Statistical analyses

Behaviourial observations were quantified by, i) tallying the number of trials demonstrating each behaviour, and ii) the number of times each behaviour was observed in a trial. Logistic regression was used to test whether the occurrence (presence/absence) of titillation and striking behaviours was related to male body size (midline plastron length, mm) for the spring and late summer behavioural trials. Linear regression was used to test whether male body size (midline plastron length, mm) was a predictor of the frequency of male-female interactions. In addition, linear regression was used to test for a relationship between male body size and the total counts of titillation (frequency of a courtship behaviour) and striking (frequency of a coercive behaviour) in the spring and late summer. Lastly, the occurrence (presence/absence) of shell clattering (dependent variable, defined in Appendix VI) was tested against bite duration (independent variable) in a logistic regression to further examine the co-occurrence of biting and shell clattering behaviour. All statistical analyses were completed in *R* statistical software (R Development Core Team 2013).

Results

Behaviour frequency and seasonal reproductive behaviour

In mixed-sex trials, all males approached, chased and displayed cloacal sniffing of females irrespective of male body size and season (Table 3.1). The proportions of male approach, cloacal sniffing, and chasing behavour were similar in spring and late summer (Table 3.2). Titillation was generally rare, representing a small contribution to the overall proportion of male reproductive behaviours (0.70 %) in the spring and late summer.

Similarly, biting occurred in approximately the same low proportions (0.20 %) in both seasons. In the spring, striking behaviour was observed 3.5 times more often than titillation (Table 3.2). Head biting occurred at approximately the same frequency as titillation in the spring (Table 3.2). The relative proportions of male striking and shell clattering behaviour increased by approximately 3-fold in late summer compared to spring. Striking was observed in 39% (7/18) of spring trials and 71% (20/28) of late summer trials. By contrast, titillation was less common, being observed in only 11% (2/18) of spring trials and 21% (6/28) of late summer trials. In late summer, males adopted aggressive charging (Appendix VI) directed toward females, a behaviour not seen in the spring (Table 3.1, Table 3.2). Two of the 18 males in the spring trials and two of the 28 males in the late summer trials demonstrated both titillation and striking (Table 3.3). One male (ID 0620 tag, 1424 notch), used in both spring and late summer trials, showed a higher frequency of titillation in spring but a higher frequency of striking in late summer. Males did not show any clear orientation preference when striking at females (Table 3.4). In general, lateral strikes were most common, followed by frontal, dorsal, and ventral. All observations of male biting were directed at the head and neck of females. Biting of the shell, limbs, and tail was never observed in mixed sex trials.

Females demonstrated foreclaw display on five occasions, but only in the late summer trials. In one case a female reciprocated foreclaw display initiated by a male. In the other four cases, a female approached the male and began foreclaw display, eliciting no reaction from the male in each case. Foreclaw display was never observed between females.

Male body size and reproductive behaviour

Reproductive tactics used by males varied with body size and season. In spring, male body size was not a significant predictor of titillation ($z_{17} = 0.031$, $p = 0.975$, Figure 3.2a) or striking ($z_{17} = 1.154$, $p = 0.249$; Figure 3.2b); however, in the late summer, small males were significantly more likely to demonstrate titillation ($z_{28} = -1.945$, $p = 0.052$; Figure 3.2 c), whereas large males were significantly more likely to strike at females ($z_{28} = 2.694$, $p < 0.01$ (Figure 3.2d).

An increase in male body size was associated with a significant decrease in the frequency of titillation in late summer ($R^2 = 0.37$, $t_{27} = -3.96$, $p < 0.0005$; Figure 3.3b), but not in spring ($R^2 = 0.062$, $t_{16} = 1.15$, $p = 0.27$, Figure 3.3a) when titillation was already rare. The frequency of male striking increased significantly with body size in spring ($R^2 = 0.36$, $t_{16} = 3.019$, $p < 0.01$; Figure 3.3c) and late summer ($R^2 = 0.27$, $t_{27} = 3.169$, $p < 0.005$; Figure 3.3d). Mean body size of males demonstrating titillation was 102.15 mm ($n = 7$) and the mean body size of males demonstrating striking was 124.72 mm ($n = 23$) (Table 3.5). The logistic (Figure 3.2) and linear regression plots (Figure 3.3) indicate a threshold body size of approximately 100 mm plastron length that divides male behaviours; titillation was used by males < 100 mm and striking was used by males > 100 mm.

Male body size was not related to the total number of male-female interactions in either spring ($R^2 = 0.17$, $t_{16} = 1.82$, $p = 0.087$) or late summer ($R^2 = 0.027$, $t_{26} = -0.84$, $p = 0.41$) (Figure 3.4). However, there was a trend towards larger males interacting more with females in spring and smaller males interacting more with females in late summer (Figure 3.4).

Description of male aggression and shell clattering behaviour

Males struck at and bit the head and neck of females from dorsal, lateral, and ventral orientations. Ventral strikes involved males approaching females from behind, pausing to sniff the cloacal or inguinal region (on occasion), and diving under females before re-approaching from below to strike at the throat.

Bite duration was highly variable, from as short as 3 seconds to nearly 600 seconds (Table 3.6). Of the 16 bites observed, most were on the female's dorsal head/neck, followed by bites on the lateral head/neck, frontal on the head/jawline, and on the throat/ventral neck (Table 3.6). Males were significantly more likely to engage in shell clattering the longer they bit a female (z_{15} =6.01, $p < 0.0001$). Males demonstrated shell clattering while biting females in open water and while resting on the substrate (see video recordings, Appendix VII). Following restraint by male biting, females responded by open mouth gaping and violent struggling. Females also swam backwards, attempted to withdraw into their shells, and extended their forelimbs to push the aggressor male away and dislodge his jaws. In response to female struggling, males regularly used their forelimbs to clear the obstructive forelimbs of the female and engage in shell clattering. Shell clattering resulted in an audible knocking that could be heard from up to 2 m away. An individual shell clattering episode typically took place over 3-5 second intervals and was characterized by three clatters ("knocks", Kramer 1984) in rapid succession. Continuous shell clattering events lasting over 10 seconds and 15 or more successive clatters were observed.

When a pair came to rest on the substrate during biting, the male rocked back-and-forth on his hindlimbs with the anterior edge of his shell (anterior marginal and cervical scutes) inside the anterior shell opening of the female. This rocking motion appeared to grind the serrated anterior marginal scutes and projecting cervical scute of males (Chapter I) against the head/neck of females. Injuries from this rocking motion were evident on the dorsal neck of females as broad lacerations and sometimes associated with wounds from the tomiodonts (see Chapter II, Figure 2.9a). During shell clattering, the anterior marginal scutes and cervical scute of the male would be driven into the head and neck of the female. In some cases, shell clattering resulted in the female's head being struck against the anterior edge of her own carapace, especially when a male bit the throat and shell clattered from a ventral position. After being released from a long bout of biting (331 sec), forced submergence, and violent shell clattering (111 clatters), a female (ID 182 tag) appeared temporarily stunned, disoriented, and was relatively slow to surface (Appendix VII, Video A.7). Post-trial evaluation occasionally revealed fresh wounds on females (Figure 3.5). The origin of these wounds was later confirmed by observations of male biting behaviour during video review. Biting did not always result in external wounds, suggesting that wounding estimates (Chapter II) may be conservative in terms of the frequency of male coercion. In at least one example, a female sustained internal injury with bleeding from the mouth and internal nares (Figure 3.6). After extended periods of biting, males released their bite for no apparent reason. Males did not demonstrate mounting or copulation following biting, forced submergence, or shell clattering.

Behaviour summary of intrasexual trials and female aggression

Three complete and one incomplete all-male trial (90-minute duration) and one all-female trial were conducted in the late summer to assess intrasexual aggression. Male-male aggression was present (Table 3.7; 3.75 strikes/trial, 0.25 bites/trial, $n = 3$ complete, 1 incomplete trial), although it occurred at a lower frequency compared to male-female aggression from late summer trials (5.89 strikes/trial, 0.25 bites/trial, $n = 28$ complete trials). Males commonly displayed neutral behaviour toward each other, such as approach and sniffing, and did not participate in intrasexual titillation. Intrasexual aggression among males took the form of charging, striking, and a single instance of biting (Table 3.7). Consistent with observations from intersexual trials, larger males demonstrated aggressive behaviour more often than smaller males and typically directed this behaviour at the next largest male in the trial (Table 3.7). Overt aggression was not observed in the all-female trial, although the largest female in the trial did open-mouth gape on three occasions when accidently bumped by other females in the enclosure. During the intersexual trials of the spring and late summer, aggression between females was very rarely observed. In the over 100 hours of video recordings, a female was observed charging another female on only three occasions and striking at another female on only three occasions. Likewise, female aggression towards males was rare with only three observations of a female charging a male and two observations of a female striking at a male. Females were never observed biting or shell clattering.

Late season male activity patterns

Observations and recapture data collected at the Arowhon sites in August and September 2013 showed a shift in the capture sex ratio from a strong female-bias to a male-bias towards the end of the active season. The female:male sex ratio significantly declined during late summer sampling ($R^2 = 0.40$, $t_{18} = -3.366$, $p < 0.01$; Figure 3.7).

Discussion

Summary of findings

Consistent with my prediction, males employ their tomiodonts in aggressive interactions with females by biting leading to forced submergence, and shell clattering, during the reproductive seasons. Apparent reproductive behaviour in the Arowhon population of *C. picta* was observed in both spring and late summer. A higher frequency of male reproductive behaviour, particularly coercive behaviour, occurred in late summer. Male size was a significant predictor of titillation (courtship behaviour) and striking (coercive behaviour) in late summer, but not in spring. Males less than 100 mm in plastron length tended to court females using titillation, whereas males greater than 100 mm in plastron length employed coercive tactics, such as striking, when interacting with females. Mounting and copulation were not observed following either courtship or coercive tactics. Aggression by male *C. picta* resulted in injuries to females. All biting by males was directed at the head and neck of females, although there was no clear preference for a specific location on this region. Female-female aggression was rare, whereas male-male aggression was observed between the largest males.

Late summer is the primary reproductive season of C. picta in Algonquin Park

My behavioural trials demonstrated heightened male reproductive activity, particularly aggressive intersexual behaviour, in late summer. An increasing frequency of male reproductive activity and male conspicuousness (Figure 3.7), and elevated rates of female wounding (Chapter II) provide evidence that late summer is an important breeding period for the Arowhon *C. picta*. I suggest that late summer (and perhaps autumn) is the primary breeding period for Arowhon *C. picta*. To verify this suggestion, further field observation, behavioural trials, and female cloacal flushing to check for the presence of sperm will be necessary.

As discussed in Chapter II, the beginning (spring) and end (late summer and autumn) of the active season have been recognized as periods of breeding activity for *C. picta* (Taylor 1933, Finneran 1948, Sexton 1959, Gibbons 1968*a*, Moll 1973, Licht *et al*. 1985, Gist *et al*. 1990, Krawchuk and Brooks 1998, Ernst and Lovich 2009). Despite study since 1978, the breeding season of the Arowhon *C. picta* population has not been well investigated. Personal observations suggest that Arowhon male *C. picta* are active earlier in the year (*i.e*., emerge earlier from winter dormancy) and remain active later in the season. These observations are consistent with seasonally male-biased activity in *Trachemys scripta* (Morreale *et al*. 1984, Thomas *et al*. 1999) and *Chelydra serpentina* (R.J. Brooks, pers. comm. 2014). By extending the length of their active season, males can increase mate-searching activities, improve their chances of successful mating, and thereby increase their reproductive fitness (Morreale *et al*. 1984, Thomas *et al*. 1999). A gradient in reproductive activity/timing would be expected in *C. picta* because of

latitudinal differences in the length of the active season (Christiansen and Moll 1973, Moll 1973, Thomas *et al*. 1999). Southerly populations have more favourable conditions (resource availability and a longer active season), likely promoting reproductive activity at both the beginning and end (or throughout) the active season. However, the need to pay off potential overwintering energy debt and the narrow time window between emergence from overwintering (late April) and nesting (early June), could mean that Algonquin *C*. *picta* (especially reproductive females) forgo energetically costly mating activity in the spring. Thus, thermal and energetic constraints imposed by a northern climate (Koper and Brooks 2000, Rollinson and Brooks 2007, 2008*b*) may restrict primary breeding activity to the fall in Algonquin *C*. *picta*.

The first record of shell clattering in C. picta

My study is the first to report shell clattering in *C*. *picta*. Kramer (1984, 1989) coined the term "shell clattering" in *Pseudemys nelsoni* stemming from two observations of a male biting the hindlimb of a female. During extended periods of biting (>7 minutes), the males demonstrated rapid and repeated extension and retraction of their neck resulting in the forceful contact of the male and female shells. The striking of the two shells together produced an (underwater) audible knock. Clattering took place in 3-5 second intervals with 5-15 individual knocks repeated in succession. Following biting and shell clattering, the male *P*. *nelsoni* uneventfully released the female and did not attempt copulation. The observations made by Kramer (1984, 1989) with *Pseudemys* closely parallel those reported here for *C*. *picta*. The extended bite duration, clattering frequency, clattering duration, and an absence of copulatory behaviour post-biting in *P*.

nelsoni are consistent with my *C. picta* observations. *Chrysemys* and *Pseudemys* are closely related (Seidel and Smith 1986, Stephens and Wiens 2003, 2009) and both taxa share a number of reproductive behaviours with other members of Emydidae, *e.g.*, *Trachemys* and *Graptemys* (Seidel 2002, Stephens and Wiens 2003, Ernst and Lovich 2009). Just as titillation is found in a number of emydid taxa (*Chrysemys*, *Pseudemys*, *Trachemys*, *Graptemys*), shell clattering may too be present and simply underreported. To the best of my knowledge, shell clattering has only been reported previously for *P. nelsoni* (Kramer 1984, 1989).

Functional significance of titillation and foreclaw display in emydids

In my behavioural trials, male titillation display was infrequently observed and largely restricted to smaller males. In addition, female *C. picta* initiated foreclaw display with males. Although titillation appears to serve a role in male emydid courtship, the other contexts in which foreclaw display has been observed suggest that it is not solely for courtship. Thomas and Altig (2006) make the well-grounded distinction between titillation and foreclaw display stating that the former should be reserved as a description of reproductive behaviour and the latter represents a non-reproductive communicative behaviour. Others have suggested that foreclaw display may function in species or individual recognition (Jackson and Davis 1972, Kramer 1989, Kramer and Burghardt 1998), as a reproductive isolating mechanism (Jackson and Davis 1972), in information gathering about novel objects (Cagle 1955), in the establishment and maintenance of social dominance (Rives 1978), and/or in precocious courtship and play (Kramer and Burghardt 1998). Juvenile foreclaw display has been reported in *Graptemys, Pseudemys*,

Trachemys, and *Chrysemys* (Cagle 1955, Wahlquist 1970, Morris 1976, Petranka and Phillippi 1978, Rives 1978). Young emydids display in the presence of food and at inanimate objects (Cagle 1955, Morris 1976, Rives 1978). Captive juvenile *Chrysemys* initiate foreclaw display intra- and interspecifically (Rives 1978). Foreclaw display has been observed between adult male *Chrysemys picta* (Gibbons 1968*a*, Taylor 1933, Rives 1978), between adult male *Trachemys scripta* (Cagle 1950), and in interspecific pairings of these species in captive and natural settings (Rives 1978). Adult female emydids display to one another (Jackson 1977) and in response to the display of males (Wahlquist 1970, Ernst 1971*a*, Zappalorti 1976, Lovich *et al*. 1990, this study). In *Trachemys*, female foreclaw display was more frequently directed at females than males, did not peak during the mating period, and did not result in copulation (Thomas and Altig 2006).

Male body size and aggression

In my behavourial trials, smaller male *C*. *picta* demonstrated courtship behaviour via titillation, whereas larger males demonstrate coercive behaviour toward females, such as striking and biting. Others studying the reproductive tactics of emydid turtles have also found a shift in reproductive behaviours with male size. For example, only small male *Pseudemys nelsoni* performed courtship and titillation, whereas larger males were prone to biting and aggression toward females (Lardie 1983, Kramer 1986, 1989). Similarly, male *Trachemys scripta* show size-dependent alternative mating tactics; larger *T*. *scripta* have a much higher precopulatory display rate coupled with chasing and biting relative to the low precopulatory display rate and titillation courtship of smaller males (Thomas 2002). Body size is a significant predictor of biting propensity in juvenile, adult female,

and adult male *T. scripta* (Hites *et al*. 2013). Indeed, biting is well-established in the behavioural repertoire of chelonians in general. Jackson and Davis (1972), followed by Liu *et al*. (2013), compiled a non-exhaustive list of 21 and 27 chelonian species, respectively, that demonstrate biting during courtship. Most of the species listed as biting during courtship fit the criteria outlined by Berry and Shine (1980) as being semi-aquatic or bottom walking and demonstrating a male-biased body size. But *Chrysemys picta* and *Trachemys scripta* (among other emydid taxa) are both free-swimming open water species with a larger female body size than males and males that demonstrate an elaborate courtship display early in their reproductive life. Why then would males adopt coercive tactics at a large adult size? Below, I propose a theory to explain the evolution of coercive mating tactics in emydid turtles, with a focus on *C. picta*.

Why would coercive tactics be advantageous?

Titillation can be energetically costly, time consuming, and does not always result in copulation (Jackson and David 1972, Kramer 1989, Pearse *et al*. 2002, Kramer and Burghardt 1998; current study). If coercion is a more time efficient mating tactic than courtship, coercive males have the potential to mate with more females in a given period of time. Coercion would not be a successful tactic for smaller males because their small size/mass prohibits them from forcing a larger female to copulate (*C. picta* has female-biased size dimorphism; Ernst and Lovich 2009; this study). Aggressive tactics may serve as an indicator of male strength, affirm social dominance, or cue receptivity in females (Kramer 1986). Social hierarchy may be present in *C. picta* based on observations of dominance in captive settings (Ernst and Lovich 2009) and aggressive interactions

between basking individuals (Bury *et al*. 1979). A lower intensity of coercive behaviour by smaller males may limit their reproductive potential (Sacchi *et al*. 2005). Males that exhibit coercive tactics potentially have a lot to gain, even from a single copulation. The ability of female *C*. *picta* to store sperm for several years can secure a male's paternity for multiple clutches from a single copulation (McTaggart 2000, Pearse *et al*. 2002, Hughes 2011, McGuire *et al*. 2014).

Recall that some episodes of biting and forced submergence approached 10 minutes in duration (Table 3.6). The combination of rigorous struggling and high female metabolism (from late summer follicular development; Congdon and Tinkle 1982, Mitchell 1985, Rollinson nad Brooks 2008*a*, *b*, Rollinson *et al*. 2012) can induce hypoxia in submerged females. I propose that males using coercive tactics, such as biting and submergence, to force females into a dichotomous cost trade-off: breathe or breed. If the costs of remaining submerged (*e*.*g*., hypoxia, drowning) are greater than the costs of mating, a female will allow a male to copulate. However, if females resist coercion, males may be forced to release their bite and surface should they instead become oxygen limited, as may have been the case in my trials.

Lastly, males may use coercion because it results in increased reproductive fitness relative to titillation. Recall that larger females had more wounds (Chapter II) and that larger males are more aggressive. Size-dependent assortative mating may be taking place if large males target large fecund females with coercive behaviours in order to maximize their reproductive pay-offs. Using data collected in behavioural trials, a future study should examine the sizes of males and females to see if males prefer larger females because of their higher fecundity (MacCulloch and Weller 1988, Congdon and van Loben

Sels 1991, 1993, McTaggart 2000, Rollinson and Brooks 2008*b*). Biting, forced submergence, and shell clattering did not result in immediate copulation. Nevertheless, coercive male behaviour involving harassment and intimidation can function to increase female sexual co-operation in the future (Goodall 1986, Smuts and Smuts 1993, Andersson and Iwasa 1996).

Why adopt coercive tactics? A theory of female preference, proportional male foreclaw length, and reproductive success in Arowhon C. picta

Females often demonstrate a preference for a particular trait(s) or behaviour(s) in a mate (Arak and Enquist 1993, Andersson 1994), and these traits form the basis of female mate choice (Jennions and Petrie 1997). Males that demonstrate this trait or behaviour are preferred mates, compete well against other males for mating opportunities, and may experience higher reproductive fitness (Darwin 1871, Fisher 1915, 1958). The more extreme a male's phenotype, the better able he is to exploit female preference, gain more mating opportunities, and sire more offspring (Andersson 1982, Ryan and Keddy-Hector 1992, Ryan and Cummings 2013). Maintaining preferred traits and behaviours can be costly for males in terms of energetics and impaired survival, although well-endowed males may benefit from high mating success (Darwin 1871, Zahavi 1975, 1977). Female mate preferences can have profound effects on the direction and strength of sexual selection acting on males (Jennions and Petrie 1997), and thereby the evolution of male dimorphic traits and reproductive tactics.

The elongate foreclaws and titillation courtship display of some male emydid taxa are derived reproductive characters, having evolved hypothetically to assist in female

acquiescence, and to supersede ancestral biting tactics during courtship (Jackson and Davis 1972, Liu *et al*. 2013). Growth of the foreclaws in emydids is a testosterone mediated process (Evans 1946, 1951, 1952). Foreclaw elongation in *Chrysemys* begins at the onset of sexual maturity (Gibbons 1968*a*, Gibbons and Greene 1990, Frazer *et al*. 1993, Ernst and Lovich 2009), which occurs at approximately 90 mm plastron length in Arowhon male *C*. *picta* (Samson 2003). Male foreclaws demonstrate rapid growth and elongation at maturity (Samson 2003), but foreclaw growth soon slows and becomes isometric in adulthood (Chapter I). Relative to body size, small males have proportionately larger foreclaws than large males (Figure 3.8).

Male aggression is costly for females because it may drive females away from optimal foraging areas, reduce their time available for necessary activities (*e*.*g*., feeding, basking), create costs to heal wounds, and increase risk of secondary infection from wounds (Chapter II). Suppose that female *C*. *picta* (in the Arowhon population) demonstrate a strong preference for elongate foreclaws and a non-aggressive titillation courtship display. Given that smaller males demonstrate more exaggerated ornaments (foreclaws), small males would be better able to exploit this female preference during courtship. Small males would represent the extreme forelimb claw phenotype most sought after by females. As a result, young males may be highly competitive compared to larger (proportionately less ornamented) males when courting females. In effect, as male *C*. *picta* "grow into" their foreclaws they may experience a decline in attractiveness to females. If larger males experience a decline in reproductive success because females no longer find them attractive, I suggest that large males adopt coercive reproductive tactics to circumvent female choice in an attempt to maintain reproductive success. Thus an

ontogenetic shift in male *C. picta* reproductive tactics from courtship to coercion is expected if males experience a decline in reproductive success (with age or size) under a female mate choice mating system. In this scenario there are two competing mating tactics: i) small males courting, exploiting a female preference for elongate forelaws and/or their display, and mating through female choice, and ii) larger males employing coercion and trying to maintain reproductive success despite declining attractiveness to females.

Coercive reproductive tactics, population density, and sex ratio

Environmental conditions, such as population density and operational sex ratio (ratio of sexually active males and females, Andersson 1994), influence mating system dynamics. Mate competition is expected to intensify with increasing population density and operational sex ratio skew, particularly when the sex ratio is male-biased (Krupa and Sih 1993, Rowe *et al*. 1994, Cureton *et al*. 2010, Székeley *et al*. 2014). The Arowhon *C. picta* population density estimates are low compared to estimates reported from other areas in the species' range (see overview by Ernst and Lovich 2009, p. 210). As a result, population density is not likely to play an important role in the coercive reproductive tactics of Arowhon male *C. picta*.

Operational sex ratio is purported to be a strong driver of mating behaviour because it dictates the intensity of intrasexual competition and mating opportunity (Clutton-Brock and Parker 1992, Kvarnemo and Ahnesjo 1996). In water strider (*Gerris* spp.) mating systems, a male-biased sex ratio is associated with a greater per capita harassment rate of females, decreased female mating resistance, and an increase in the

probability of male mating, mating frequency, and mating duration (Clark 1988, Arnqvist 1992, Rowe 1992, Krupa and Sih 1993, Rowe *et al*. 1994, Weigensberg and Fairbairn 1994). Most researchers report adult *C*. *picta* population sex ratios approximating 1:1 (Ernst 1971*b*, Gibbons 1968*b*, Mitchell 1988, Ross 1989, Zweifel 1989, Ernst and Lovich 2009), or relatively small male biases (1.3:1, male:female; Ream and Ream 1966) or female biases (1:1.39, male:female; Balcombe and Licht 1987). A notable male-biased sex ratio (2.3:1) has been reported from a well-studied *C*. *picta* population (McGuire *et al*. 2014). An adult sex ratio skewed toward females is less common in *C*. *picta* (Ernst and Lovich 2009). The adult *C*. *picta* sex ratio at the Arowhon sites is strongly female biased (3.44:1, female:male; Samson 2003). Could the aberrant Arowhon sex ratio be related to coercive male reproductive tactics? Why would males employ coercive reproductive tactics in a population with an apparent over-abundance of females, when intrasexual competition is presumed to be low?

Consider first a scenario with an even (1:1) male:female sex ratio. In a population with an even sex ratio, every female has a "partner" in theory (although in reality, not all males mate), therefore the chances of encountering an unmated female is rare. Dominant or preferred males may mate with multiple females and exclude other males from participating in reproduction. Given high male-male competition, the chances of a male siring a whole clutch (or even the majority of a clutch) are low because a female likely has multiple partners. Now, consider a male-biased sex ratio. Male-male competition for mates is more intense as females are increasingly limited. Again, there is a high likelihood that multiple males will mate with a single female making the siring success of a single male quite small. A given male is likely to have low reproductive fitness,

especially if dominant or preferred males displace subordinate males from reproduction. In this scenario, reproductive pay-offs are relatively low overall. Lastly, consider a female-biased sex ratio as seen in the Arowhon population (3.44:1 adult female:male, Samson 2003). Female-biased populations offer reduced competition for mates, more available females, and a greater likelihood of monopolizing offspring paternity. There are many more females than males, thus not every female is "partnered". When males are limiting, females cannot afford to be too choosy. Also, consider that any given male may employ courtship and/or coercive mating tactics. Titillation tactics are lengthy and do not guarantee successful copulation even after extended periods of courtship (see below). If coercive tactics (female harassment and forced insemination) increase the frequency of copulation and/or decrease the pre-copulatory time associated with each female, a male can increase reproductive success and mate with more females in a given time period. In *C. picta*, the second male to mate often takes precedence in clutch paternity (Pearse *et al*. 2002). Long-term sperm storage in female *C. picta* (McTaggart 2000, Pearse *et al*. 2002, Hughes 2011, McGuire *et al*. 2011, McGuire *et al*. 2014) and high rates of repeat within-year and among-year clutch paternity (McGuire *et al*. 2011, McGuire *et al*. 2014) means that a single male C. *picta* has a lot to gain relative to other males, even from a single copulation. If coercive tactics have even a slightly higher rate of successful copulation and are more time efficient compared to courtship, then coercion offers greater reproductive pay-offs. Thus, whatever tactic a male uses in a female-biased population his siring success is "good" (relative to even sex or male-biased sex ratio), but his siring success may be best when he utilizes coercion.

Arowhon paternity data: a preliminary theoretical test

Offspring parentage in the Algonquin Park *C. picta* population has been examined on two previous occasions (McTaggart 2000, Hughes 2011). Both investigators tested male body size and forelimb claw length as characters used by females for mate choice. Forelimb claw length, predicted to be an indicator of male quality, did not influence male reproductive success (McTaggart 2000, Hughes 2011). Interestingly, both investigators reported that successful males were smaller than average in body size; however, their results were not identical. McTaggart (2000, 23 pp.) reported that reproductively successful males had a smaller body size than non-successful males, whereas Hughes (2011, 26 pp.) reported that successful males did not differ in size from unsuccessful males, but that among successful males, those that sired multiple clutches were significantly smaller than those that sired only a single clutch. The greater siring success of smaller males is consistent with my hypothesis that females prefer small males demonstrating courtship.

On the contrary, paternity studies in an Illinois population of *C. picta* found no evidence of size difference between reproductively successful and unsuccessful males (Pearce *et al*. 2002). However, if both courtship and coercive reproductive tactics result in successful copulation (presumably each tactic would have to be successful to remain in the population), the distribution of siring males would appear to span all body sizes, from small courting males to large coercing males. In the case of Pearse *et al*. (2002), where both small and large males sired offspring, the presence of alternative competing tactics may exist but appear masked due to the apparent continuum of reproductive success with

male body size. Courtship and coercive reproductive tactics could co-exist in a population. A female preference for smaller courting males interrupted by the coercive tactics of larger males would indeed establish a complex interaction of paternity and mating tactics that would be difficult to tease apart.

An inverse relationship between proportional foreclaw length and tomiodont size in C. picta

Foreclaws of *Trachemys* grow very slowly or cease growth all together post-maturity (Terrell and Garstka 1984, Lovich *et al*. 1990). Consistent with Thomas' (2002) findings in *Trachemys*, the reduced investment in foreclaw growth and the declining use of titillation with size (and/or age) suggest that the importance of the foreclaws in reproduction wanes with size and/or age.

In Chapter I, I showed that post-maturity male *C. picta* experience isometric foreclaw growth and strong positively allometric tomiodont growth. A striking relationship emerges when one examines the proportional size of the foreclaws and tomiodonts relative to body size in *C. picta* (Figure 3.8). The proportional size of the foreclaws significantly decreases with body size ($b = -5.25 \times 10^{-4}$, $t_{68} = -6.00$, $R^2 = 0.35$, $p < 0.0001$), whereas the proportional size of the tomiodonts significantly increases with body size ($b = 8.56 \times 10^{-5}$, $t_{68} = 3.72$, $R^2 = 0.17$, $p < 0.001$). This inverse relationship suggests a shifting investment in secondary sexual traits from the foreclaws to the tomiodonts with body size. Just as recently mature male *C. picta* demonstrate foreclaw elongation for use in titillation, can the strong positively allometric growth of the tomiodonts be related to the onset of striking and biting behaviour in larger (older)

males? The ontogenetic shift in investment from foreclaws to tomiodonts (Figure 3.8) coincides with a shift in reproductive behaviour from courtship to coercion (Figure 3.2). In short, large males have large tomidonts and demonstrate an elevated frequency of coercive behaviours including striking, biting, forced submergence, and shell clattering toward females.

Testosterone as a proximate mechanism of coercive behaviours

There is reason to suspect that circulating testosterone may be higher in larger males demonstrating coercive behaviours. Plasma testosterone in *C. picta* has been shown to peak two to three weeks following winter emergence and rise again in September coincident with spermatogenesis (Licht *et al*. 1985). Turtles with high levels of testosterone are more active (Evans 1940*a*) and more dominant (Evans 1940*b*) than conspecifics. Just as testosterone is responsible for foreclaw elongation (Evans 1946, 1951, 1952), testosterone may also be important for regulating tomiodont growth and coercive reproductive behaviours. Testosterone implant experiments, as have been conducted for foreclaw growth studies (Evans 1946, 1951, 1952), could be used to test this hypothesis.

Methodological considerations

Recall that no acclimation period was provided between the time that turtles were added to the trial enclosures and the time that behaviourial evaluation began. Reproductive behaviours, including approach, cloacal sniffing, and striking, were observed within the first minute of trials. I believe that the short handling time and

naturalistic setting of the trials allowed turtles to resume typical behaviours shortly after introduction into a trial. Nevertheless, I would recommend that future researchers using a similar trial set-up should include a brief acclimation period. Also, a larger sample size of intrasexual trials, particularly male-male trials, will be necessary to better understand social dynamics and the importance of intrasexual aggression.

The two-hour trial period in my experiment may not have been long enough to observe copulation. Pre-copulatory pursuit and courtship by male emydids is lengthy (Jackson and Davis 1972), lasting hours to days (Kramer 1989, Kramer and Fritz 1989) and potentially even weeks (Ernst 1971*a*). Despite extensive underwater field observations (~150 hours) involving male titillation and coercion, Kramer (1989) still did not observe copulation in wild *Pseudemys*. Future researchers may wish to extend the length of the trial period.

Future directions

In Chapter III, I demonstrated the functional significance of male *C. picta* tomiodonts as part of a sexually coercive behavioural repertoire; males use tomiodonts to bite females during the reproductive season. This provides evidence of coercive reproductive tactics in *C. picta* and lends further support for my hypotheses regarding the male-biased tomiodont dimorphism and female wounding presented in Chapter I and Chapter II, respectively.

Researchers examining *C. picta* paternity have assumed female mate choice (McTaggart 2000, Pearce *et al*. 2002, Hughes 2011) and a male trait(s) that is a direct measure of quality. Although females may demonstrate mate choice by selecting smaller

males as mates (at least there appears to be some inclination in the Arowhon population), coercion and forced insemination by larger male *C. picta* may have obscured such a trend in past work. Despite all the work to characterize male *C. picta* foreclaws in relation to paternity, researches have neglected foreclaw function. A detailed analysis of *C. picta* titillation sequence is called for.

Combining morphological parameters (*e.g.*, foreclaw length, proportional foreclaw length, foreclaw symmetry, body size, tomiodont length, tomiodont splay angle) with paternity analysis, and behavioural assessments would make a powerful study of male *C. picta* reproductive success. Although this work would be difficult given the cryptic reproductive behaviour of aquatic chelonians, I believe that many of the findings would be novel and contribute greatly to our understanding of chelonian mating systems. Known age individuals from the long-term population monitoring at the Arowhon sites provide a unique opportunity for a direct test of male age (rather than just male size) and female age (Congdon *et al*. 2003) and mating tactics. Additional paternity analyses in the Arowhon population are essential to address outstanding questions of male reproductive success. My assessment of the behavioural trials was one-sided given that I did not consider female behaviours. In order to further address questions of male mating tactics, it is essential that female behaviours be examined. Reviewing the trial data to assess male preference of females is also a necessary next step.

I suspect that coercive male *C. picta* reproductive tactics observed at the Arowhon sites are not a unique phenomenon. The presence of titillation and coercive reproductive tactics in closely related *Trachemys* (Thomas 2002), *Pseudemys* (Kramer 1984, 1986, 1989), and now *Chrysemys* indicates that emydid turtles do not necessarily fit the female

choice mating system (Berry and Shine 1980) that has long been ascribed to this group. Consistent with others (Gibbons and Lovich 1990, Bels and Crama 1994), I conclude that Berry and Shine's (1980) separation of "forced insemination bottom walking chelonians" and "mate choice courting free-swimming aquatic chelonians" is overly simplistic, albeit a good coarse division in reproductive tactics. As a group with a long evolutionary history and extant phylogenetic and ecological diversity, (emydid) turtles are a fascinating group in which to ask questions about mating system evolution. There are great strides to be made using turtles, especially *C. picta*, as models of sexual selection theory.

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Table 3.1: Occurrence of male Painted Turtle (*Chrysemys picta*) reproductive behaviours during spring (n = 18) and late summer (n = 28) mixed sex behavioural trials, Arowhon population, Algonquin Provincial Park. [a] represents a behaviour that was also seen in one of the incomplete trials. [b] represents a behaviour that was also seen in two of the incomplete trials.

Reproductive behaviour	**Spring trials** (/18)	**Late summer trials** (/28)
Neutral		
Approach	100% (18)	100% (28)
Chase	100% (18)	100% (28)
Cloacal sniff	100% (18)	100% (28)
Mount	0% (0)	0% (0)
Copulation	0% (0)	0% (0)
Courtship		
Titillation	11% (2)	21% (6)
Coercion		
Bite (body)	0% (0)	0% (0)
Bite (head)	17% (3[a])	14% (4[a])
Charge	0% (0)	29% (8[a])
Forced submergence	6% (1)	14% (4)
Shell clattering	11% (2)	11% (3)
Strike	39% (7)	71% (20[b])

Table 3.2: Cumulative frequency of male Painted Turtle (*Chrysemys picta*) reproductive behavioural interactions during spring (n = 18) and late summer (n = 28) mixed sex behavioural trials, Arowhon population, Algonquin Provincial Park. The numbers in parentheses represent additional observations from the two incomplete trials (< 2 hours) in each the spring and late summer. Percentage calculations exclude incomplete trials and may not add to 100% due to rounding.

Reproductive behaviour	**Spring trials**	**% spring behaviours**	**Late summer trials**	**% summer behaviours**
Neutral				
Approach	831 (42)	53.6	1714 (77)	54.9
Cloacal sniff	376 (10)	24.3	636 (20)	20.4
Mount	0 (0)	0	0 (0)	0
Copulation	0 (0)	0	0 (0)	0
Courtship				
Titillation	11 (0)	0.71	22 (0)	0.70
Coercion				
Bite (body)	0 (0)	0	0 (0)	0
Bite (head)	3 (1)	0.19	7 (1)	0.20
Charge	0 (0)	0	43 (16)	1.40
Chase	269 (10)	17.4	335 (24)	10.7
Forced submergence	1 (0)	0.065	4 (0)	0.10
Shell clattering	34 (0)	2.2	196 (0)	6.3
Strike	24 (11)	1.6	165 (17)	5.3

Table 3.3: Male Painted Turtles (*Chrysemys picta*) demonstrating both courtship (titillation) and coercion (striking) during a single trial. Note that Male ID 0620 tag (T), 1424 notch (N) displayed a greater frequency of titillation than striking in the spring behavioural trials, switching to a greater frequency of striking than titillation in the late summer behavioural trials.

Trial #	Male ID	Midplastron length (mm)	No. titillation	No. strike
7 Spring	0620T, 1424N	134.1	10	5
21 Spring	1160T, 1249N	102.1	1	1
11 Late Summer	0184T, 0070N	134.8	1	1
31 Late Summer	0620T, 1424N	134.1	1	5

Table 3.4: Occurrence of male *C. picta* strike behaviour directed toward females during spring and late summer behavioural trials (Arowhon population, Algonquin Provincial Park). The numbers in parentheses represent additional observations from the two incomplete trials (< 2 hours) in each of the spring and late summer. Note that the total number of trials with observed strikes is a count of the occurrence of strike behaviour in a trial, not a cumulative count of strikes from each male position.

	Spring trials			**Late summer trials**		
Male strike position	**No. trials with observed strikes (/18)**	**% trials with observed strikes**	**Total no. strikes observed**	**No. trials with observed strikes (/28)**	**% trials with observed strikes**	**Total no. strikes observed**
Dorsal	5 (1)	28 (6)	11 (1)	12 (1)	43 (4)	20 (5)
Ventral	1	6	1	14 (2)	50 (7)	21 (1)
Lateral	3 (1)	17 (6)	5 (9)	7 (1)	25 (4)	74 (7)
Frontal	3 (1)	17 (6)	7 (1)	8 (2)	29 (7)	50 (4)
Total	7 (2)	39 (11)	24 (11)	20(2)	71 (7)	165 (17)

Table 3.5: Male Painted Turtle (*Chrysemys picta*) body size (midline plastron length, mm) in relation to titillation, striking, and both titillation and striking behaviours. Data combined (without replicates) for the spring and late summer behavioural trials.

	Male behaviour		
Summary parameters	**Titillation**	**Striking**	**Both**
No. males demonstrating behaviour	7	23	3
Minimum body size	87.84	102.10	102.10
Maximum body size	134.80	146.50	134.8
Mean body size	102.15	124.72	123.67
Std. dev. body size	37.89	23.98	18.68

Table 3.6: Summary of male Painted Turtle (*Chrysemys picta*) biting and shell clattering behaviour during spring and late summer behaviour trials. Identification of each male denoted by tag ID (T) and notch ID (N). Note that male E13T, 1893N was run in one incomplete and one complete trial in the spring of 2013. Bite location denoted by dorsal (D), lateral (L), frontal (F), and ventral (V). [a] represents an incomplete trial (<2 hours).

Trial #	Male ID	No. bites	Bite location	Bite duration (s)	No. shell clatters
7 Spring	0620T, 1424N	1	D	7	0
10 Spring [a]	J48T, 0301N	1	L	3	0
11 Spring [a]	E13T, 1893N	4	D; D; D; D	27; 20; 20; 432	0; 0; 0; 31
20 Spring	184T, 0070N	1	F	7	0
24 Spring	E13T, 1893N	1	L	597	31
1 Late Summer [a]	0379T, 0902N	1	L	4	0
2 Late Summer	J48T, 0301N	1	F	11	0
3 Late Summer	0188T, 1553N	1	L	44	3
17 Late Summer	0857T, 1555N	2	D; V	29; 7	0; 0
18 Late Summer	0197T, 0276N	2	F; F	4; 507	0; 82
22 Late Summer	0811T, 1711N	1	V	331	111

Table 3.7: All-male (n = 4) and all-female (n = 1) behavioural trials assessing intrasexual aggression in Painted Turtles (*Chrysemys picta*), Arowhon population, Algonquin Provincial Park. [a] Male X31T bit male 1049T on the right forelimb and held on for 4 seconds. [b] Incomplete trial (90 minute duration).

Trial #	Turtle ID	Midplastron length (mm)	No. strikes	Strike(s) directed at
27 Late Summer, all-male	0184T	134.8	2	A366T
	A366T	124.9	1	0184T
	1409N	113.0	0	-
	1659N	109.74	0	-
33 Late Summer, all-male	1049T	137.7	1	X31T
	X31T	134.7	7	1049T[a], 1503N, 1411N
	1503N	109.1	0	-
	1411N	108.3	0	-
35 Late Summer, all-male	1011T	124.0	2	1409N, 0810T
	0810T	117.2	1	1608N
	1409N	116.0	0	-
	1608N	106.0	0	-
36 Late Summer, all-male[b]	0188T	141.9	0	-
	J48T	138.8	1	0188T
	0811T	134.7	0	-
	0197T	129.1	0	-
34 Late Summer, all-female	B14T	153.4	0	-
	0181T	139.2	0	-
	0151T	130.5	0	-
	7031(B)N	101.3	0	-

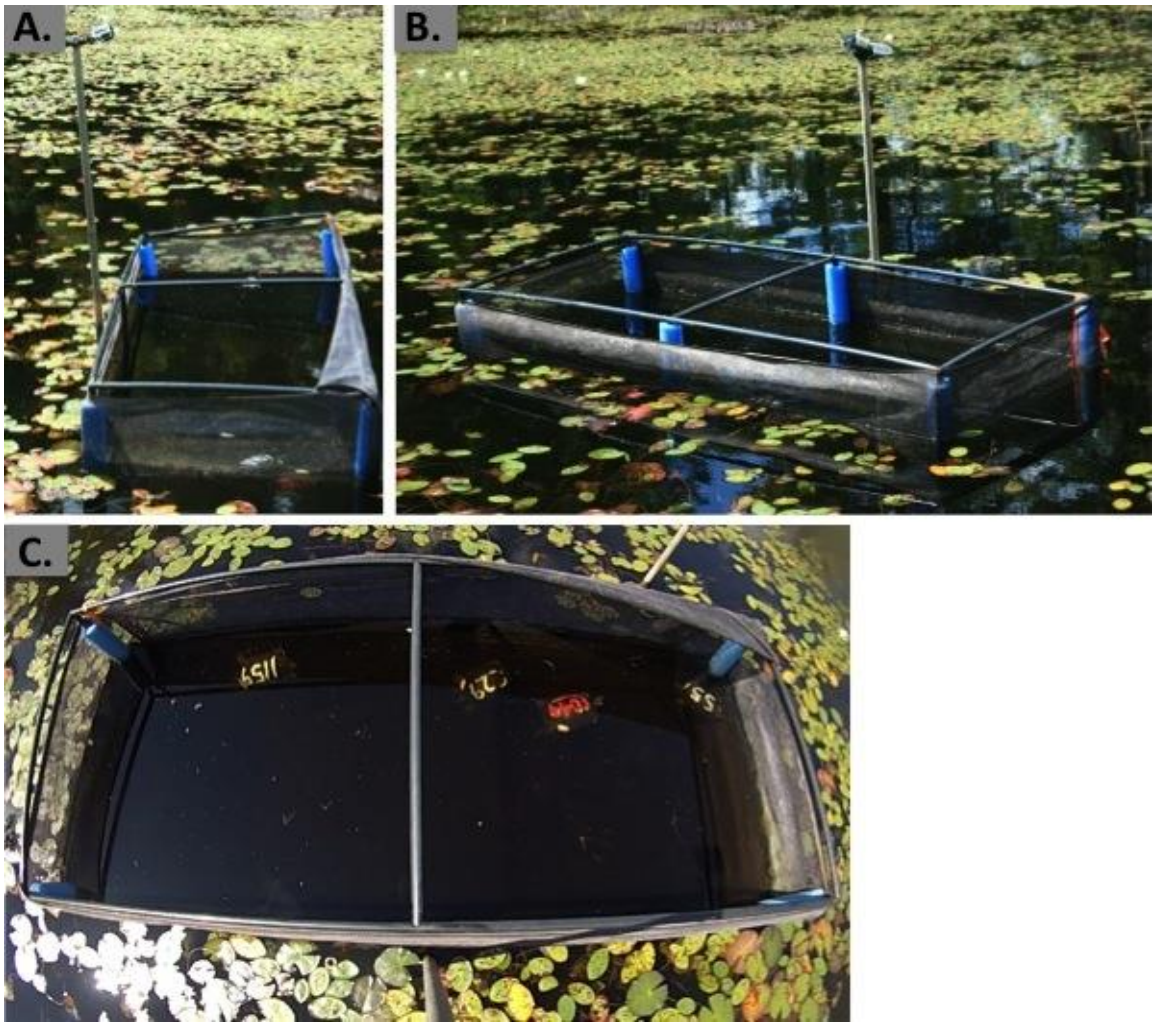

Figure 3.1: *In situ* behavioural trial enclosure for the study of male Painted Turtle (*Chrysemys picta*) reproductive behaviour; A) side view, B) lateral view, and C) camera view. Trial enclosures were constructed of lightweight PVC frame, fitted nylon mesh walls, and measured 183 cm long x 76 cm wide x 76 cm deep (adapted from Exo-Terra® Flexarium, full screen terrarium, Rolf C. Hagen Inc., Montreal). Enclosures were submerged at a depth of ~60 cm. Floatation devices (in blue) were placed at each corner to elevate the upper frame out of the water and prevent turtle escape. A GoPro® camera is mounted mid-way along the length of the enclosure.

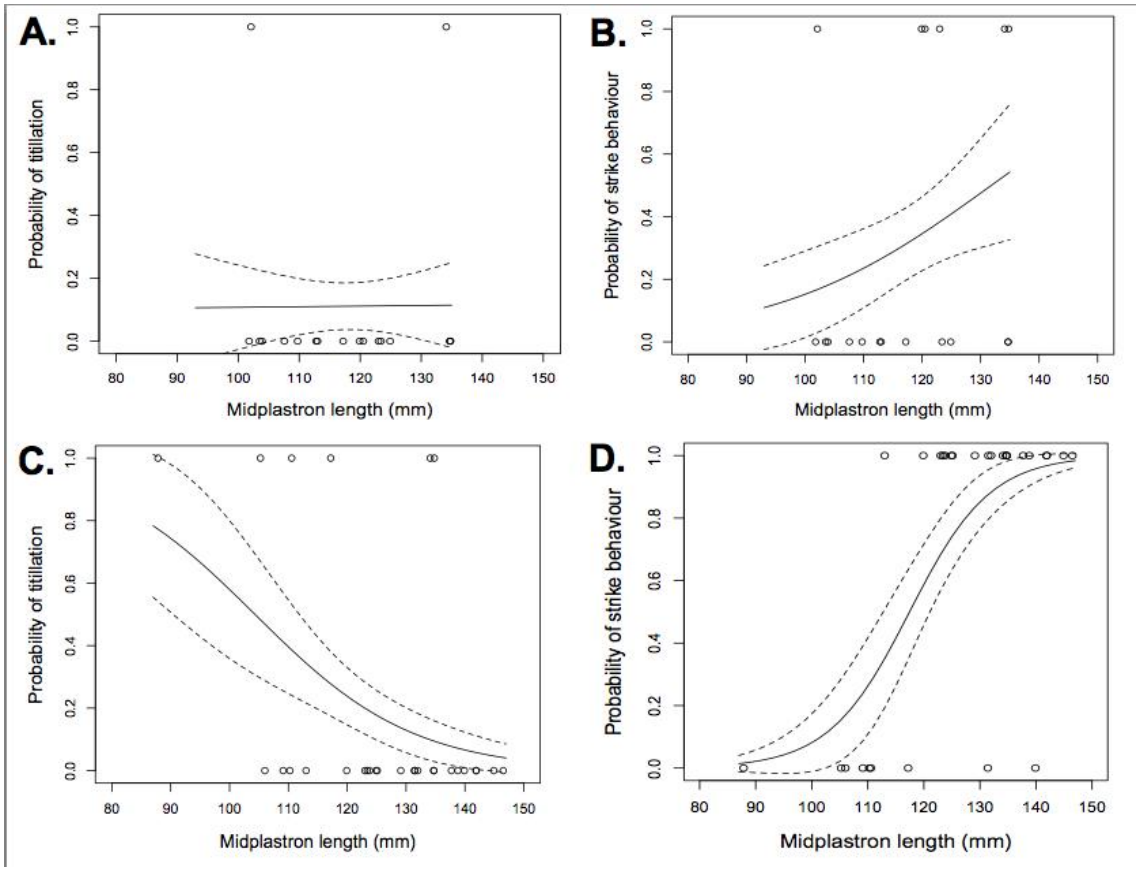

Figure 3.2: Male Painted Turtles (*Chrysemys picta*) body size and the presence or absence of titillation (courtship) behaviour and striking/biting (coercive) behaviour in spring and summer behavioural trials (logistic regression). A. titillation behaviour in spring trials; B. striking behaviour in spring trials; C. titillation behaviour in late summer trials; D. striking behaviour in late summer trials.

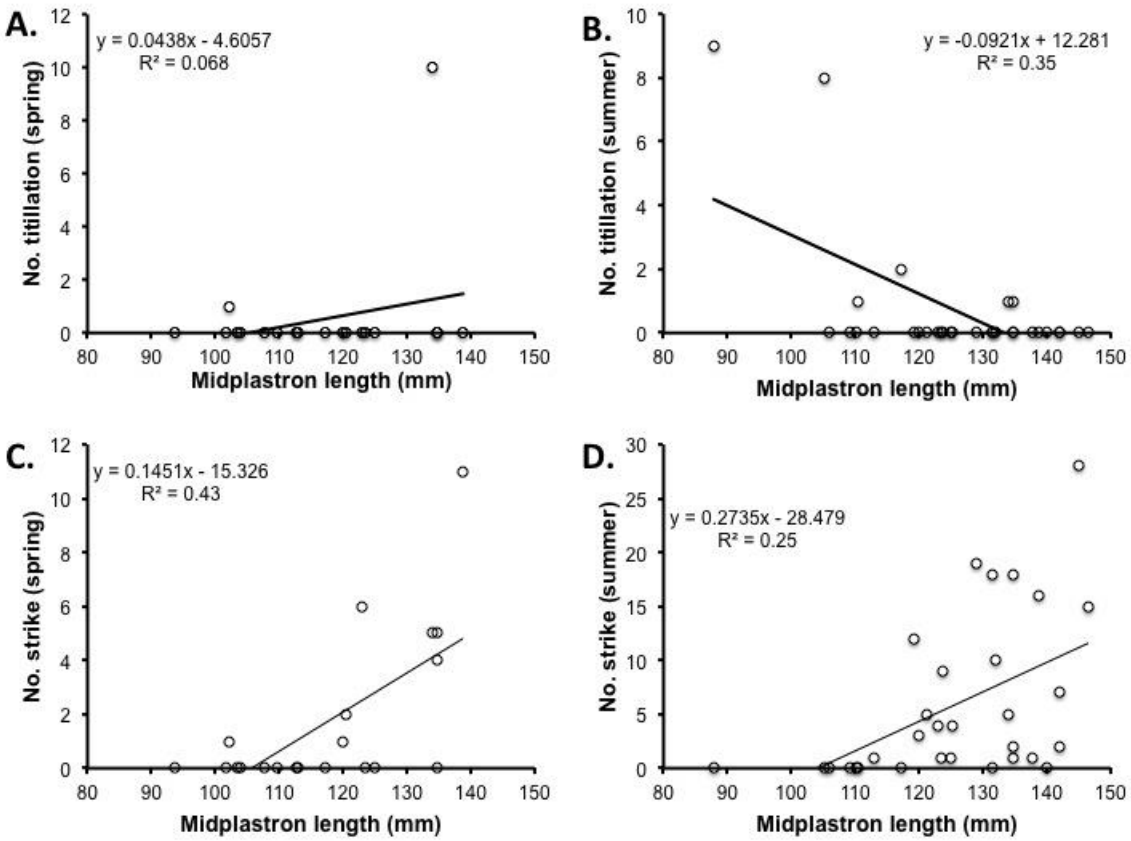

Figure 3.3: Male Painted Turtle (*Chrysemys picta*) body size (midplastron length, mm) and the frequency of courtship (titillation) behaviour in A.) spring and B.) late summer. Male Painted Turtle (*Chrysemys picta*) body size (midplastron length, mm) and the frequency of coercive (striking) behaviour in C.) spring and D.) late summer. Note difference in y-axis scales.

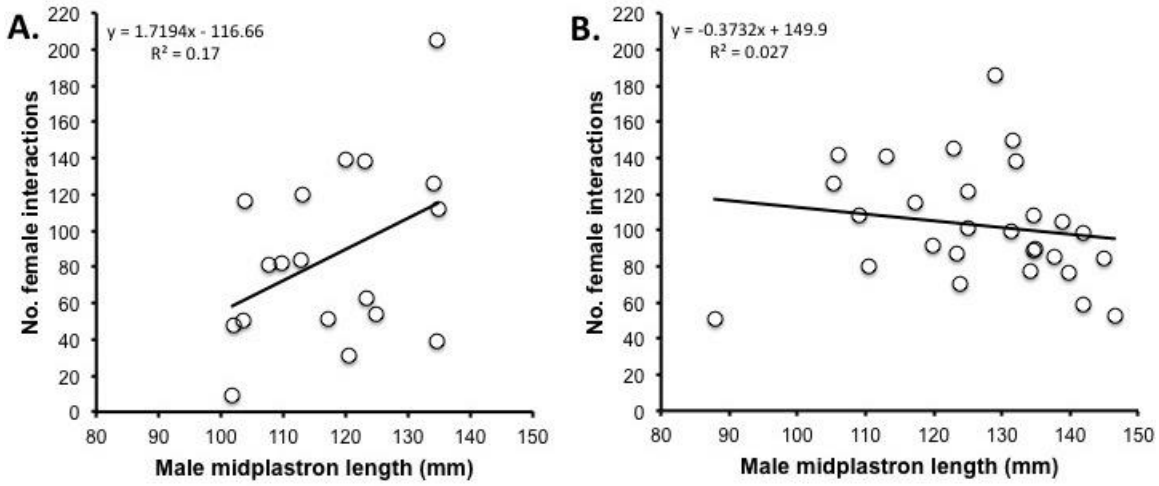

Figure 3.4: Relationship between male Painted Turtle (*Chrysemys picta*) body size (midplastron length, mm) and the total number of male interactions (all behaviours combined) with females in the A.) spring and B.) late summer.

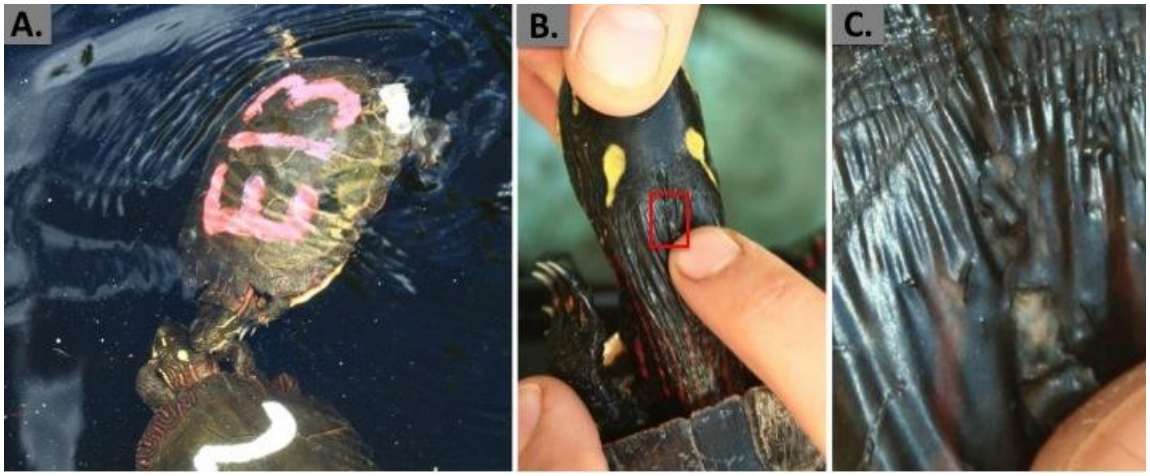

Figure 3.5: Male coercion and female wounding from spring Trial #11 (incomplete recording). A.) Male Painted Turtle (*Chrysemys picta*) ID E13 tag (1983N) biting the dorsal head of female ID 0024T (0729N). Female ID 0024T (0729N) demonstrated open mouth gaping and exhibited strong resistance against the coercive behaviours of male ID E13 tag (1983N), including attempts to withdraw her head into her shell, struggling, backward swimming, and pushing the male away with her forelimbs (seen in photo). The male maintained this bite for 432 seconds, forcefully submerging the female and engaging in shell clattering during this time. B.) Post-trial evaluation revealed a discrete fresh wound on the dorsal neck of Female ID 0024T (0729N) consisting of C.) numerous short, shallow gashes and a flap of skin. The width between the fresh wound gashed approximated the tomiodont gap width of male ID E13 tag. Male *C. picta* ID E13 tag (1983N) has the largest tomiodonts in the study (see Chapter I) and repeatedly displayed aggressive behaviour toward females (Table 3.6). See Appendix VII, Video A.2 for spring Trial #11 video clip demonstrating coercive behaviour (striking, biting, shell clattering) of male ID E13 Tag (1893 notch) directed at female ID 0024 tag (0729 notch).

Figure 3.6: Injuries of female ID 1184 tag (0215 notch) Painted Turtle (*Chrysemys picta*) following late summer Trial #18 with male ID 197 Tag (0276 notch). A) frontal head of male *C. picta* male ID 197 Tag (0276 notch) demonstrating well-defined tomiodonts. B) Post-trial evaluation revealed a subtle fresh wound (circled) on the right lower jaw of female ID 1184 tag (0215 notch) who was bitten by male ID 197 Tag (0276 notch) during late summer Trial #18. C) Female ID 1184 tag (0215 notch) also experienced bleeding from the internal nares and D) blood pooling at the posterior corner of the right jaw as a result of aggression from male ID 197 Tag (0276 notch). See Appendix VII, Video A.6 for late summer Trial #18 video clips demonstrating coercive behaviour (striking, biting, shell clattering) of male ID 197 Tag (0276 notch) directed at female ID 1184 tag (0215 notch).

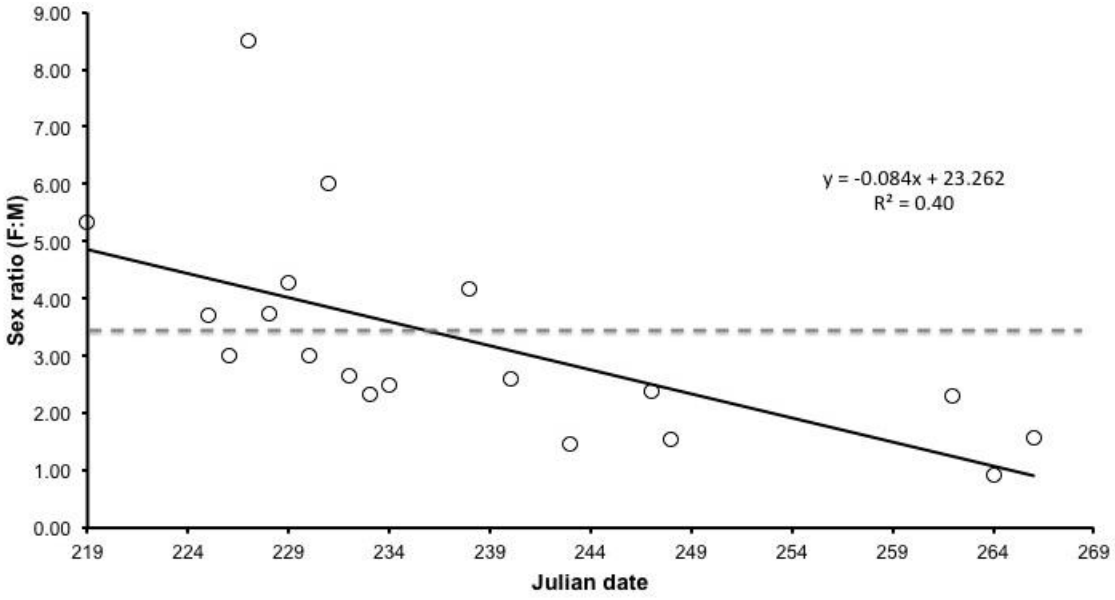

Figure 3.7: Late summer capture sex ratio of Arowhon population Painted Turtles (*Chrysemys picta*), Algonquin Provincial Park. Sampling period spans August 8, 2013 (Julian date 219) to September 24, 2013 (Julian date 266). Dashed line represents the population sex ratio of 3.44:1, female:male (Samson 2003).

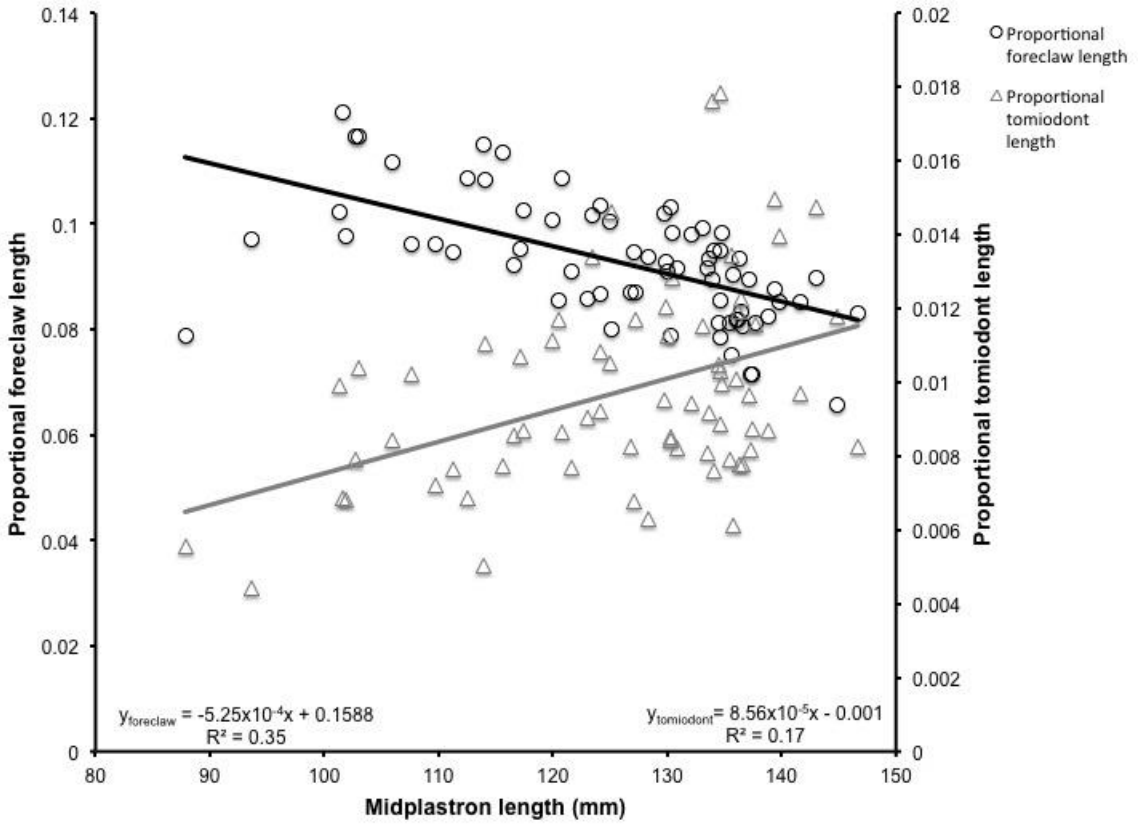

Figure 3.8: Relationship of proportional foreclaw length and proportional tomiodont length to body size (midplastron length, mm) in male Painted Turtles (*Chrysemys picta*), Arowhon population, Algonquin Provincial Park.

General Conclusions

In Chapter I, I showed that the head morphology of male and female *C. picta* differs notably, especially with respect to the tomiodonts. Male *C. picta* have a relatively longer head and rostrum (among other traits), giving their head a more angular appearance in lateral profile. The pointed snout and accompanying head dimorphisms of *C. picta* are also seen in some Sliders (*Trachemys* sp.), suggesting that these dimorphisms may be more taxonomically widespread and important than previously recognized. By examining the head morphology of juveniles, I was able to provide some basic insights into the ontogeny of head dimorphism in *C. picta*. Dietary partitioning and reproductive role hypotheses do not appear to explain the observed head dimorphism. I instead proposed a sexual selection hypothesis, suggesting that the tomiodonts of male *C. picta* function as sexual weapons used to coerce females into mating. The tomiodont morphology of males reflects an optimized biomechanical arrangement, ideal for bite force generation and maintaining an effective biting grip. Lastly, I suggested an additional novel dimorphism of the male *C. picta* anterior carapace, namely the serrated anterior marginal scutes and projecting nuchal scute, whose functional significance warrants further study.

In Chapter II, I used a long-term dataset to demonstrate *C. picta* population-level trends in soft tissue wounds inflicted by conspecifics. Consistent across most of 23 years, adult females experienced more wounding than adult males or juveniles. In addition, larger females had a greater probability of experiencing wounding. Wounding was largely concentrated on the dorsal head and neck of females, consistent with what would be expected from male-female aggression during sexual coercion. Elevated rates of fresh

wounding occurred during late summer coincident with the breeding period of *C. picta*. By assessing wound demographics, I provided indirect evidence that the tomiodonts of male *C. picta* inflict injury and, by their nature, are coercive sexual weapons.

In Chapter III, I combined the two observational lines of evidence from Chapter I and Chapter II to evaluate the reproductive tactics of male *C. picta*. Through *in situ* behavioural trials, my research showed that small males court females through titillation using a foreclaw display, whereas larger males employ coercive tactics, such as striking, biting, and forced submergence. Late summer, rather than spring, appears to be the primary breeding season of Arowhon population *C. picta* in Algonquin Provincial Park. I reported a novel shell clattering behaviour in *C. picta*, only the second species of chelonian in which this behaviour has been described. My findings are contrary to the female choice mating system reported for *C. picta* and join a growing body of recent research demonstrating the importance of coercive tactics in the reproduction of male emydid turtles.

The apparent novelty of sexual coercion in a well-researched species speaks to the importance of directed study and stringent observation. A solid foundation in natural history is an absolute prerequisite for such detailed research. The evolution of mating systems in turtles, particularly the ecologically and taxonomically diverse emydids, is fascinating and an area ripe for future research. "The contrast between what we expect and what we find after careful study is often remarkable" (Brooks *et al*. 2000).

References

Brooks, R.J., Strickland, D., and Rutter, R.J. 2000. Reptiles and Amphibians of Algonquin Provincial Park. The Friends of Algonquin Park, Ontario, Canada. 48 pp.

Appendix I: Literary references to cranial morphology and anterior carapace structure of *Chrysemys picta*

Accompaniment to thesis General Introduction, section *The turtles with "teeth"*; and Chapter I, section *A novel putative carapace dimorphism in C. picta*

Table A1.1: Literary references to the cranial morphology of the Painted Turtle (*Chrysemys picta* ssp.), with emphasis on the tomiodonts, across disciplines of biological study (anatomy, natural history, phylogeny) spanning a 177 year period. Note the diversity of terminology used to describe the jawline structure. References ordered chronologically.

Literary source	Context and excerpt	Reference
Reference book	In reference to *Emys oregoniensis* HARLAN (1837), synonym of *Chrysemys picta bellii*: "Characters … head small, elongated; upper jaw bidentate." (p. 9) "The head is moderately large and elongated; the snout pointed. The upper jaw is furnished in front with two remarkable teeth, and the lower has a well developed hook" (p. 10). See Plate I from Holbrook (1936-1940) (Figure A1.1). In reference to *Emys picta* SCHNEIDER (1783), synonym of *Chrysemys picta picta*, "The head is small, but full, and rounded in front; the snout being rather obtuse than pointed. The upper jaw is entire at both sides, but is notched anteriorly. The lower jaw is slightly hooked or turned upwards in front."	Holbrook 1836-1840
Reference book	"Head moderate; upper jaw notched, with a slight process on each side of the emargination." (p. 12) See Plate V from De Kay (1842) (Figure A1.2).	De Kay 1842
Reference book	In a description of the genus *Chrysemys*, "the most prominent generic character consists	Agassiz 1857

	in a notch in front of the horny sheath of the upper jaw, on each side of which the edge of the sheath projects more or less to form lateral teeth, that are close together." (p. 438)	
Museum bulletin	In reference to *Chrysemys* skull morphology, "labial edge even, with two small close teeth quite in front." (p. 38)	Gray 1870
Museum bulletin	In reference to *Chrysemys picta*: "Head moderate; snout short, feebly projecting; upper jaw with a small median notch and a small cusp on each side, the edge not or but very slightly denticulated." (p. 72)	Boulenger 1889
Reference book	In reference to *Chrysemys picta marginata*, "upper jaw with a sharp tooth on each side of a median notch; lower jaw with a median tooth" (p. 225)	Garman 1892
Reference book	In reference to the "Western Painted Tortoise", *Chrysemys marginata* (=*Chrysemys picta bellii*), as per Agassiz (1857), "head of moderate size; snout not much projecting. Jaws with smooth cutting edge, the front with an evident notch, on each side of which is a small tooth." (p. 163)	Hay 1893
Reference book	"The notch in front of the horny sheath of the upper jaw on each side of which the edge of the sheath projects somewhat to form 'lateral teeth'." (p. 368)	Babcock 1919
Reference book	In reference to genus *Chrysemys*: "Upper jaw with a median notch, lateral to which is a small tooth-like projection; lower jaw with a small tooth-like projection which fits into the upper median notch." (p. 122) "Upper jaw with a distinct median notch which is bordered on each side by a distinct 'tooth.' Snout short, not projecting far … lower jaw but little upturned and with a small median tooth." (p. 130-131) "Upper jaw with a distinct median notch which is bordered on each side by a short but	Cahn 1937

	definite tooth … lower jaw only slightly upturned and with a median point which fits into the median notch of the upper jaw" (p. 139)	
Paper	Couplet of dichotomous key defining *Chrysemys picta bellii*, "a tooth-like projection at either side of notch." (p. 22) "Many individuals bite when handled and their jaws often are so sharp that they can remove small clean-cut segments from the hand." (p. 149)	Conant 1938
Reference book	In reference to *Chrysemys bellii marginata*, "Head moderate in size; upper jaw notched in front with a sharp tooth on either side of notch (Fig. 6, Pl. VIII)." (p. 55) Plate description for *Chrysemys picta*: "Plate VIII, details of turtles, Fig. 6. Head of painted turtle. Upper jaw notched at tip, a sharp tooth at either side of notch." See Fig. 6, Plate VIII from Logier (1939) (Figure A1.3).	Logier 1939
Reference book	In reference to *Chrysemys picta picta*, "Identification: The crushing surface of the upper jaw is narrow and there is a tooth-like projections on either side of the notch at the tip of this jaws." (p. 181) Additional comments for *C. p. marginata* (p. 183), *C. p. bellii* (p. 201) and *C. p. dorsalis* (p. 203), "Identification: In form of jaw and shape of the carapace this subspecies is similar to its close ally the Eastern Painted Turtle."	Pope 1939
Reference book	*Chrysemys* genus description: "The upper jaw is notched in front and with the notch bordered by a toothlike projection on either side."	Carr 1952

Reference book	*Chrysemys picta* description: "upper jaw notched medially and with toothlike projection on each side of the notch. " (p. 175)	Stebbens 1954
Reference book	Line illustration of "têtes de tortues, vues de face" with *Chrysemys* shown in Figure A1.4, plate drawing 1. Frontal head drawing displays well-defined cusps flanking a notch (p. 90-91). See plate drawing 1 from Mélançon (1961) (Figure A1.4).	Mélançon 1961
Reference book	In reference to *C. p. bellii*: "crushing surface of upper jaw smooth; apex of upper jaw with sharp notch flanked on either side by short projection." In reference to *C. p. dorsalis*: "Head medium in size; crushing surface of upper jaw narrow, nearly smooth; upper jaw notched in front, notch bordered by toothlike projection on either side". (p. 49)	Anderson 1965
Reference book	"Description - … the skull with a broad, complete lateral temporal arch; the notch in front of the horny sheath of the upper jaw on each side of which the edge of the sheath projects somewhat to form 'lateral teeth'." (p. 42)	Bobcock 1971
Reference book	In reference to *C. p. marginata:* "Head of moderate size, width 19 to 27.5 (mean 21.3) per cent of carapace width; snout short, bluntly pointed, nostrils terminal; cutting edge of upper jaw with midline notch bordered by two small, tooth-like projections." (p. 177)	Minton 1972
Reference book	Description of *C. p. marginata*: "tip of upper jaw notched with two tooth-like projections." (p. 33)	Johnson 1982
Paper	Use of "anterior cusp absent from median ridge of upper jaw" as a character state distinguishing genera of emydid turtles (p. 244)	Seidel and Smith 1986

	"*Chrysemys* Gray (Painted Turtles) … Diagnosis –… The upper jaw is notched in front with small cusps on each side. The alveolar surface of the upper jaw is narrow with a low median ridge." (p. 246)	
Paper	Use of "anterior cusp absent from median ridge of upper jaw" as a character state distinguishing genera of emydid turtles	Seidel and Jackson 1990
Reference book	In reference to *Chrysemys picta picta*, "Definition. … anterior jaw with a pronounced notch between 2 cusps." (p. 42)	Palmer and Braswell 1995
Reference book	Regarding *Chrysemys*: "The upper jaw has two toothlike cusps on either side of a terminal notch" (p. 212)	Harding 1997
Paper	Use of jawline cusps as a qualitative osteological character in phylogeny construction, "Anteroventral border of premaxilla: smooth (0), smooth but with notch (1), notched, notch defined by two cusps (2), or hooked beak (3)."	Stephen and Wiens 2003
Reference book	In reference to *Chrysemys picta bellii*, "Description: The upper jaw has a pair of sharp cusps flanking a notch." (p. 86)	Sheldon 2006
	Frontal head photo of *C. p. bellii* with caption, "Note the pair of cusps on the upper jaw."	
Reference database	Account for *Chrysemys picta*: "The head is moderate in size with a slightly projecting snout, and the upper jaw bears a terminal notch bordered on each side by a cusp. The broad triturating surface of the maxilla bears a weak median ridge. Both the palatine and pterygoid contribute to the upper triturating surface."	Ernst *et al*. 2006
Reference book	Description of *Chrysemys picta*: "The upper jaw has two tooth-like notches." (p. 466)	Jensen *et al*. 2008
Reference book	Couplet of dichotomous key differentiating *Chrysemys*, *Trachemys* and *Pseudemys*:	Ernst and Lovich

	"Upper jaw with a prominent notch that may or may not be bordered on each side by toothlike cusps." (p. 170)	2009
Reference book	*"Chrysemys* is unique in having a deep median notch in the maxillary beak that is flanked by a pair of sharp cusps." (p. 237)	Legler and Vogt 2013

Table A1.2: Extant species of chelonians demonstrating a notched and bicuspid jaw. List not comprehensive. The genera *Pseudemys*, *Pelusios* and *Kachuga* are of particular interest because members of these groups demonstrate variable jawline morphology (jawline notched or non-notched; deep notch, or shallow notch; beak hooked, bicuspid,). * Tomiodonts or cusp-like structures are reported for this species, although this requires further attention to confirm ** *Rhinoclemmys pulcherrima incisa* is named in reference to its notched, bicuspid tomium (Legler and Vogt 2013).

Family	Species	Reference
Emydidae	*Chrysemys picta* (*C. p. picta, C. p. marginata, C. p. bellii, C. p. dorsalis*)	Table A1.1
Emydidae	*Pseudemys nelsoni*	Jackson 2010, D. Nelson (pers. comm. 2014), Jackson *et al*. 2012
Emydidae	*Pseudemys rubrientris*	Zug 1969, Ernst and Lovich 2009, Jackson *et al*. 2012
Emydidae	*Pseudemys alabamensis*	McDowell 1964, Gaffney 1979, Leary *et al*. 2008, Ernst and Lovich 2009, Jackson *et al*. 2012
Emydidae	*Pseudemys texana*	Ernst and Lovich 2009, Jackson *et al*. 2012
Emydidae	*Terrapene nelsoni* (*T. n. klauberi*)	Minx (1996)
Emydidae	*Terrapene coahuila*	Minx (1996), D. Henderson (pers. comm. 2014)
Emydidae	*Terrapene carolina* spp. (*T. c. major, T. c. triunguis, T. c. mexicana, T. c. yucatana*)	Minx (1996)
Emydidae	*Glyptemys insulpta*	Holman and Fritz 2001, pers. obs. 2013
Emydidae	*Glyptemys muhlenbergii*	
Emydidae	*Actinemys marmorata**	Holman and Fritz 2001
Bataguridae	*Rhinoclemmys pulcherrima* (*R.p. incisa*)**	Gray 1869, Legler and

		Vogt 2013
Geoemydidae	*Rhinoclemmys areolata*	Legler and Vogt 2013
Geoemydidae	*Heosemys depressa*	Ernst *et al*. 2006
Geoemydidae	*Heosemys spinosa*	Ernst *et al*. 2006
Geoemydidae	*Heosemys grandis*	Ernst *et al*. 2006
Geoemydidae	*Heosemys* (*Siebenrockiella*) *leytensis*	Ernst *et al*. 2006
Geoemydidae	*Heosemys annandalii*	Ernst *et al*. 2006
Geoemydidae	*Hardella thurjii*	McDowell 1964, Gaffney 1979, Joyce and Bell 2004
Geoemydidae	*Morenia ocellata*	Das 2010
Geoemydidae	*Geoemyda silvatica*	Praschag *et al*. 2006
Geoemydidae	*Batagur baska*	Ernst *et al*. 2006, Praschag *et al*. 2007, Moll *et al*. 2009
Geoemydidae	*Kachuga kachuga*	Ernst *et al*. 2006, Praschag *et al*. 2007
Geoemydidae	*Kachuga dhongoka*	Ernst *et al*. 2006
Pelomedusidae	*Pelusios castaneus*	Broadley 1981, Ernst *et al*. 2006
Pelomedusidae	*Pelusios sinuatus*	Broadley 1981, Broadly and Boycott 2009, Ernst *et al*. 2006
Pelomedusidae	*Pelusios chapini*	Ernst *et al*. 2006
Pelomedusidae	*Pelusios gabonensis*	Ernst *et al*. 2006
Pelomedusidae	*Pelusios rhodesianus*	Broadley 1981, Ernst *et al*. 2006
Pelomedusidae	*Pelusios williamsi*	Ernst *et al*. 2006
Dermochelyidae	*Dermochelys coriacea*	Pritchard 1971, Ernst and Lovich 2009

Table A1.3: Literary references to anterior carapace structure in the Painted Turtle (*Chrysemys picta*), with emphasis on the nuchal bone, cervical scute, and adjacent marginal scutes. References ordered chronologically.

Literary source	Context and excerpt	Reference
Reference book	In reference to male *Emys oregoniensis* HARLAN (1837), synonym of *Chrysemys picta bellii*, "Characters. Shell suboval, greatly depressed, serrated in front, slightly emarginated behind; sternum broad, oblong, serrated anteriorly, emarginated posteriorly." "The marginal plates are twenty-five in number, those in front being longest; the nuchal, or intermediate, is elongated, narrowed posteriorly, and projecting anteriorly; the first are quadrilateral, broadest behind, and serrated in front; the second and third are also quadrilateral, and serrated anteriorly, but they are broadest in front." (p. 9) "The sternum is broad, slightly contracted in the middle, serrated in front, and emarginated behind. The gular plates are triangular in shape, with their bases directed forwards, and serrated; at their outer angles is a process, prominent, pointed, and projecting beyond the rest of the plate." (p. 10) See Plate I from Holbrook (1936-1940) (Figure A1.1). In reference to *Emys picta* SCHNEIDER (1783), synonym of *Chrysemys picta picta*, "the marginal plates are twenty-five in number, and make one entire cutting margin; the nuchal, or intermediate, is nearly a parallelogram, slightly notched or serrated anteriorly."	Holbrook 1836-1840
Reference book	In reference to *Emys picta*, SCHNEIDER (1783), synonym of *Chrysemys picta picta*, "The intermediate (nuchal) marginal plate linear, often doubly notched or bidentate in front." (p. 12)	De Kay 1842

Reference book	In reference to *Chrysemys picta marginata*, "nuchal plate long, narrow, notched in front". (p. 225) In reference to *C. p. picta*, "nuchal plate about two thirds as wide as long, notched." (p. 226)	Garman 1982
Reference book	"Anterior border of the carapace often with a few dentations; the posterior border not serrated." (p. 163)	Hay 1893
Reference book	"The nuchal shield is long and narrow with its anterior edge finely serrated. Some of the marginal plates also have serrated edges." (p. 368)	Babcock 1919
Reference book	In reference to *Chrysemys picta marginata*, "The nuchal is long, narrow, and with a definite median notch anteriorly; this may or may not be bordered on each side by a series of serrations extending on to the adjacent marginal, and these serrations may be very small or high conspicuous." (p. 129) In reference to *C. p. bellii*, "Nuchal scute elongate but quite wide in most specimens – usually wider than in *marginata*; its anterior margin is usually weakly serrate and the serrations more often than not do not extend to the adjacent marginals." (p. 139) In reference to *C. p. dorsalis*, "nuchal long and narrow, usually with a very small median notch" (p. 147) and "upper jaw with a small median notch and with a very small cusp on each side of it" (p.147).	Cahn 1937
Paper	In reference to *Chrysemys picta bellii*, "Margin entire except for the nuchal and the adjacent marginals, which may be notched or serrate anteriorly … Head medium in size and flat above. Upper jaw notched in front and with a small tooth-like projection on either side of the notch." (p. 146)	Conant 1938

Paper	"*Chrysemys* Gray (Painted Turtles) … Diagnosis – … The adult carapace is smooth (without rugosities), unkeeled, not serrated or notched posteriorly, but the cervical scute is frequently notched or projected" (p. 246)	Seidel and Smith 1986
Reference book	In reference to *Chrysemys*: "In adult painted turtles, the leading edge of the carapace frequently is jagged medially and the plastron is toothed or lobate anteriorly and finely serrated posteriorly." (p. 43)	Palmer and Braswell 1995

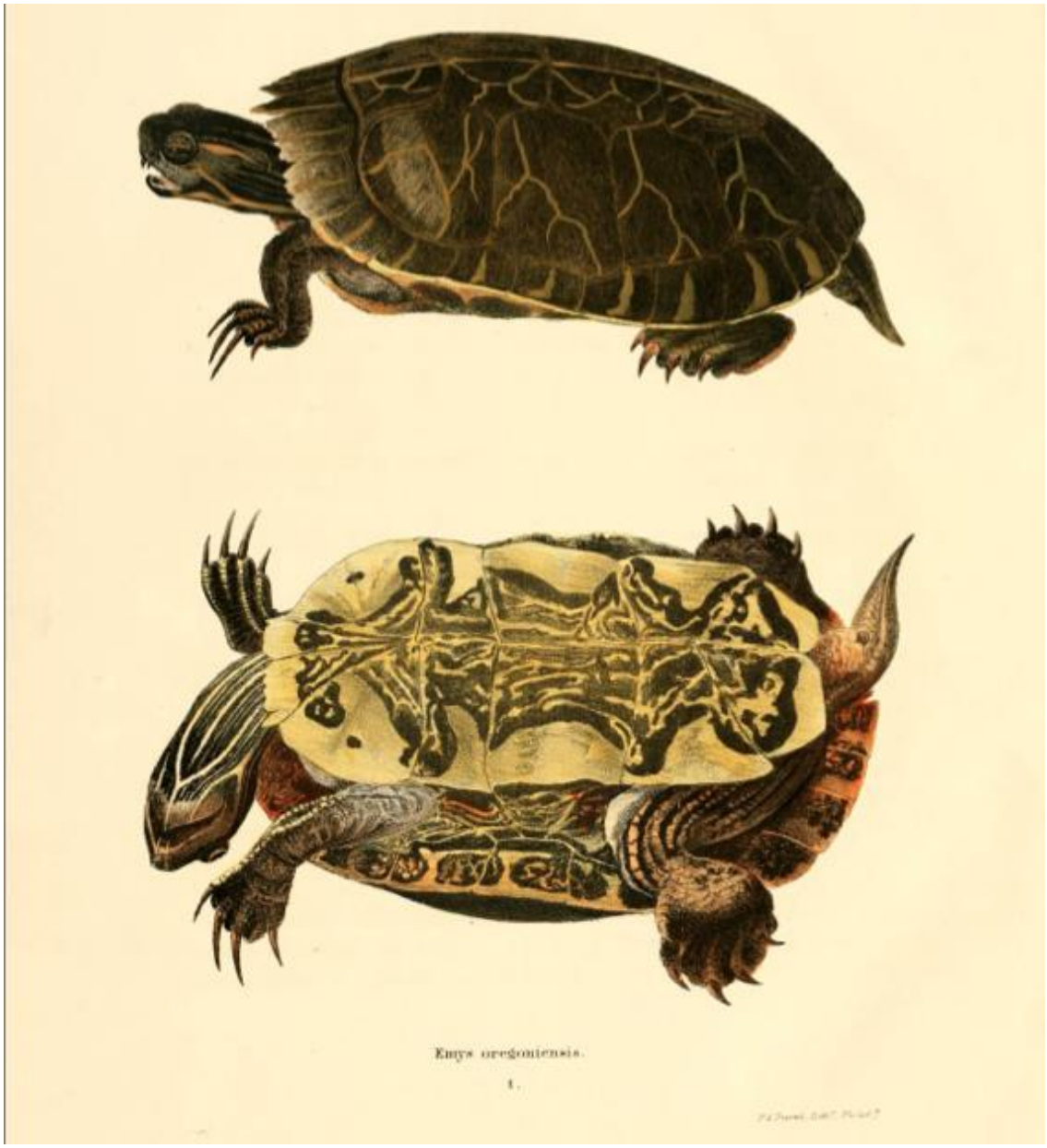

Figure A1.1: Plate I drawing of adult male *Emys oregoniensis* (=*Chrysemys picta bellii*, Western Painted Turtle) from Holbrook (1936-1940). Sex of specimen not explicitly stated by Holbrook, but inferred to be male from the elongated foreclaws and thick tail. Note the prominent tomiodonts, projecting nuchal, and highly serrated anterior marginal scutes.

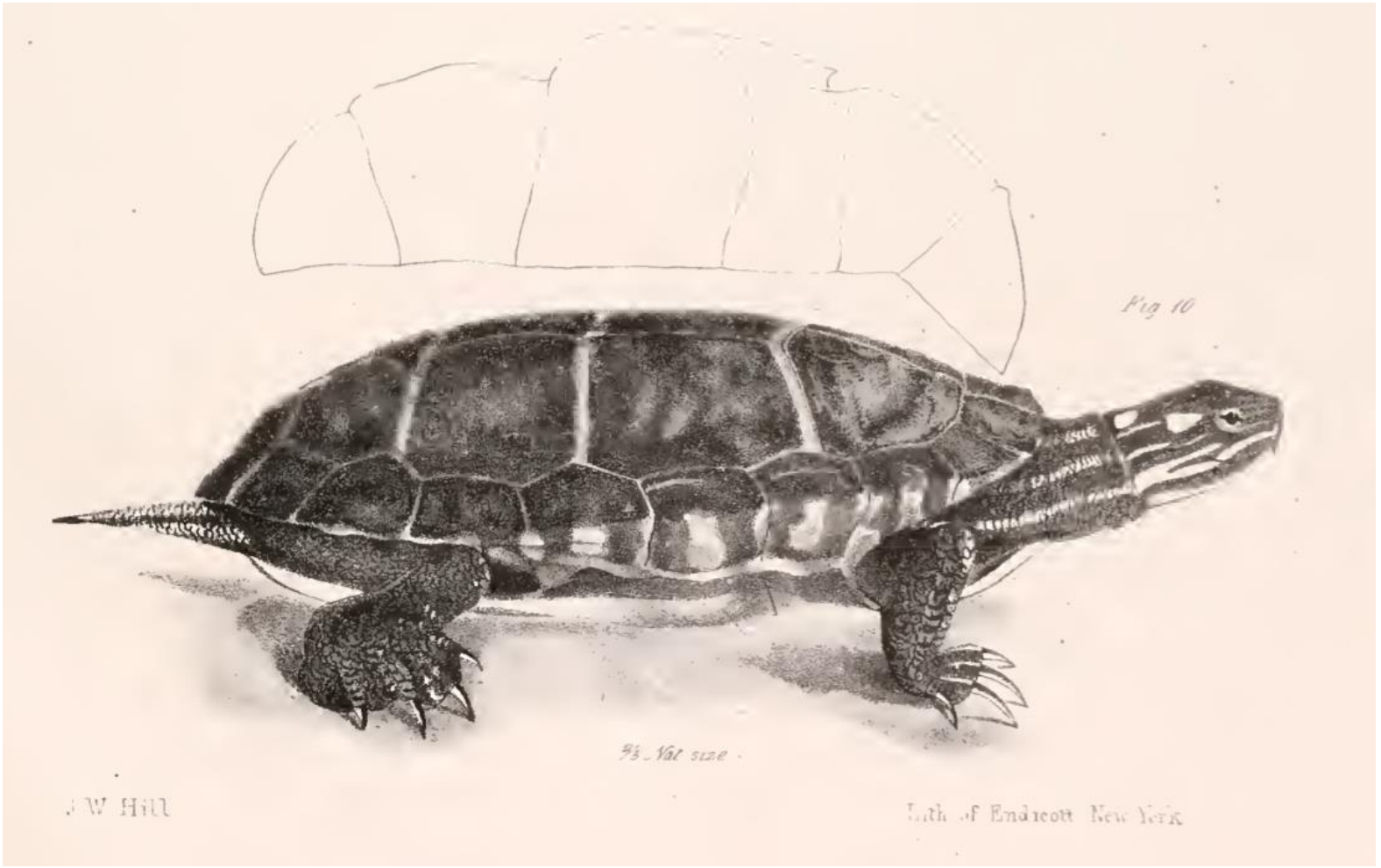

Figure A1.2: Plate I drawing of adult male *Emys picta* (=*Chrysemys picta picta*, Eastern Painted Turtle) from De Kay (1842). Sex of specimen not explicitly stated by De Kay, but inferred to be male from the elongated foreclaws (relative to hindclaws) and shallow carapace height. Note the prominent tomiodonts overhanging closed lower jaw.

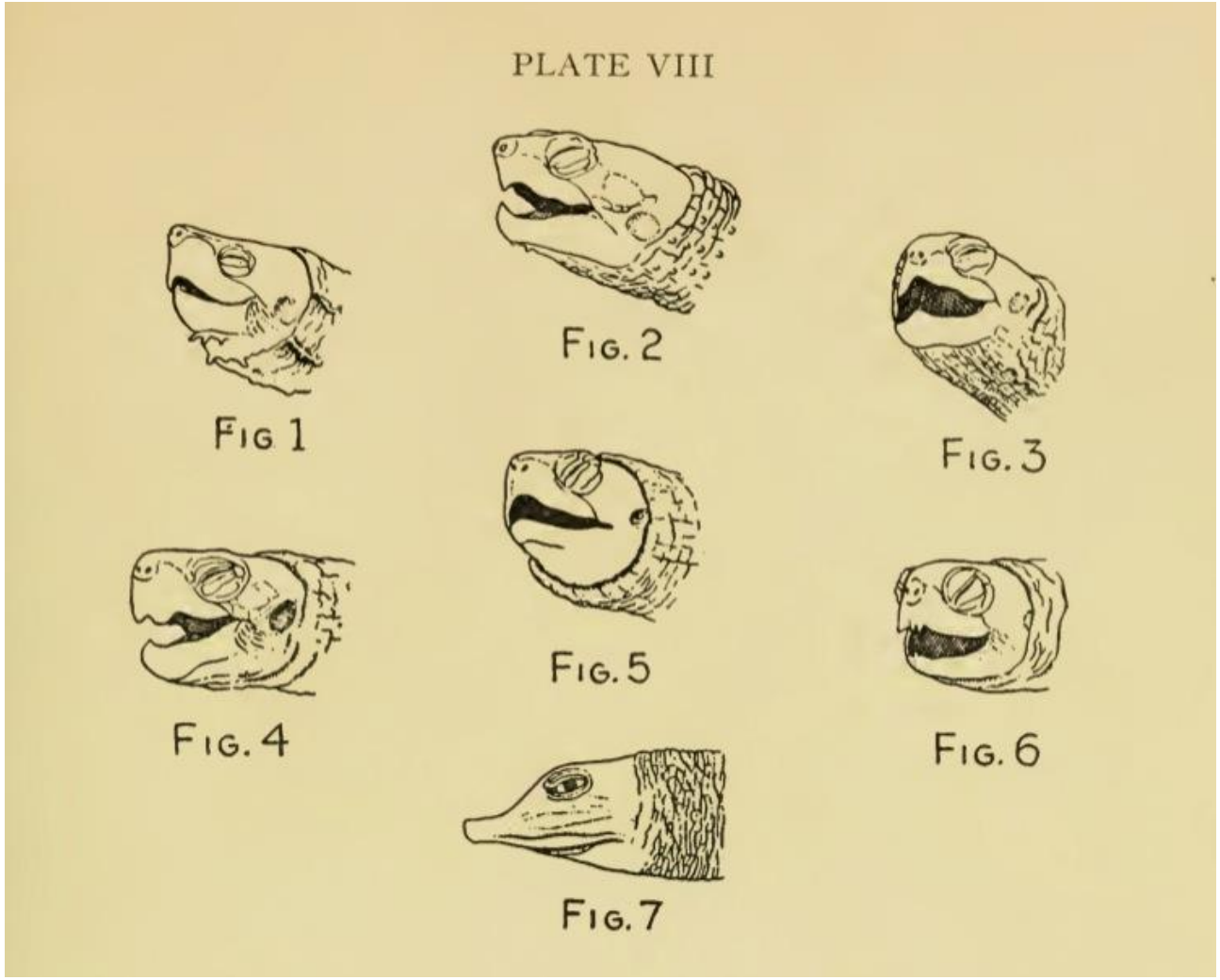

Figure A1.3: Plate VIII frontal head drawing of Ontario turtles from Logier (1939). Figure 6 representing the Midland Painted Turtle (*Chrysemys picta marginata*) with accompanying description, "head of painted turtle. Upper jaw notched at tip, a sharp tooth at either side of notch" (Logier 1939).

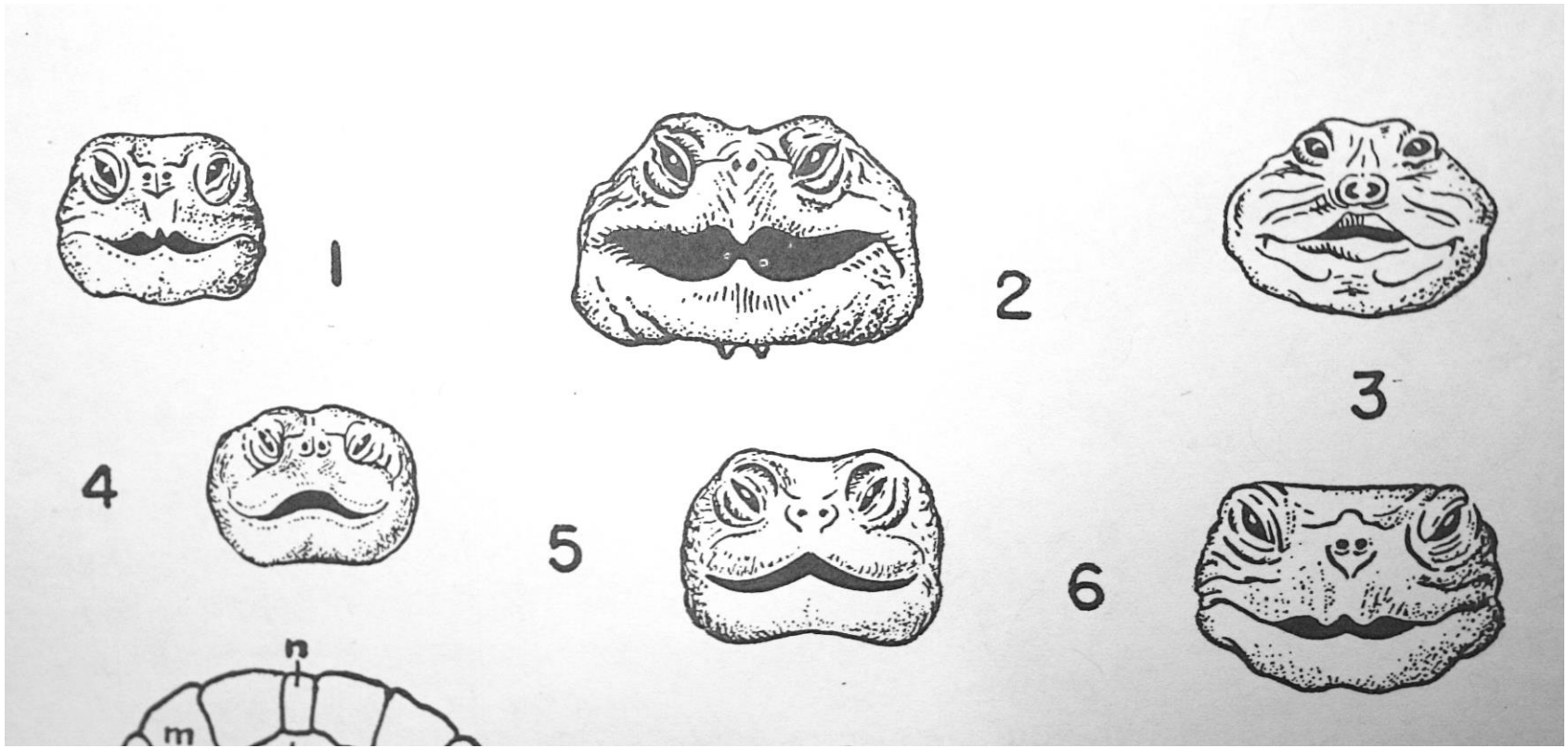

Figure A1.4: Frontal head drawing ("têtes de tortues, vues de face") of *Chrysemys picta* displaying well-defined tomiodonts flanking the central upper jaw notch (plate drawing 1). Plate drawings 1-6 from Mélançon (1961).

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Appendix II: Calculation of tomiodont length

Accompaniment to Chapter I, Methods, section *Statistical analysis*

When examined from a frontal view, the notched area between the bicuspid tomiodonts of *Chrysemys picta* resembles a triangle, often with three sides of unequal length (Figure 1).

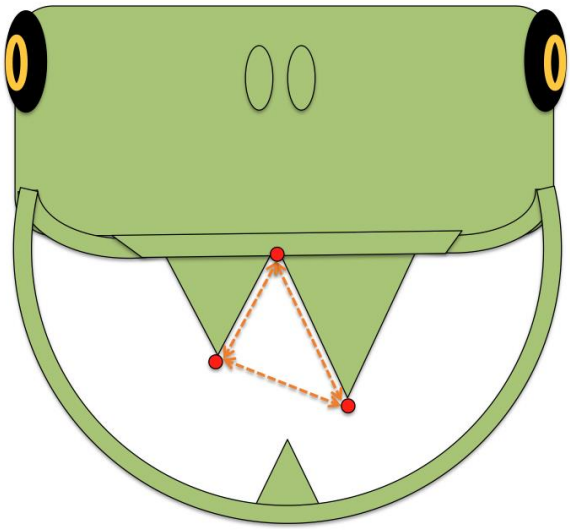

Figure A2.1: Diagrammatic frontal head view of a Painted Turtle (*Chrysemys picta*). Note the triangular area (delineated in orange) formed medially on the upper jaw by the premaxillary notch and bicuspid tomiodonts.

Consider that the left (*L*) and right (*R*) tomiodont lengths represent left and right sides of the triangle and the tomiodont gap width (*A*) represents the base of Triangle *RLA* (Figure A2.2).

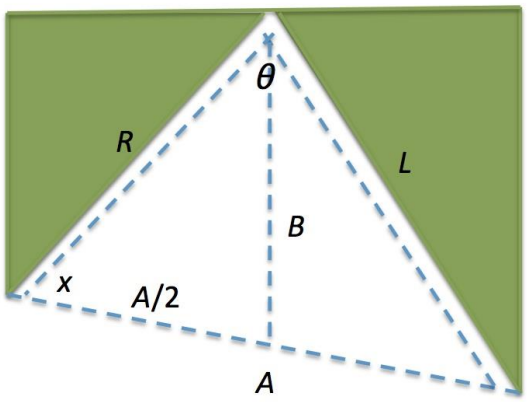

Figure A2.2: Diagrammatic frontal view of the tomiodonts of a Painted Turtle (*Chrysemys picta*). *L* = left tomiodont length, *R* = right tomiodont length, *B* = tomiodont length, *A* = tomiodont gap width, *x* = angle contained between *R* and *A*, θ = tomiodont splay, angle contained between *R* and *L*.

The Law of Cosines (Eq. 1*a*,*b*) is suitable for calculating the unknown side length of a triangle when either 1) two sides of a triangle and the contained angle are known, or 2) when all three sides of a triangle are known.

For the large triangle *RLA*, the following form of The Law of Cosines can be used to solve for unknown angle *x* given three known sides:

$$x = \arccos \frac{A^2 + R^2 \quad L^2}{2AR} \div \qquad \textbf{(Eq. 1}\boldsymbol{a}\textbf{, The Law of Cosines)}$$

For the large triangle *RLA*, the following form of The Law of Cosines can be used to solve for an unknown side (*e.g.*, side *L*) given two known sides and the contained angle:

$$L^2 = A^2 + R^2 \quad 2AR \quad \cos(x) \qquad \textbf{(Eq. 1}\boldsymbol{b}\textbf{, The Law of Cosines)}$$

Where Line *B* is forced through Line *A* at half of *A*, the Line $\left(\frac{A}{2}\right)$ results. Triangle *ALR* has now been divided into two triangles (Figure 2):

- Triangle $RB\left(\frac{A}{2}\right)$
- Triangle $LB\left(\frac{A}{2}\right)$

Take, for example, Triangle $RB\left(\frac{A}{2}\right)$. Two sides of Triangle $RB\left(\frac{A}{2}\right)$ are known, *R* and $\left(\frac{A}{2}\right)$; however, Line *B* (representing tomiodont length) is unknown. By forcing Line *B* through half of *A*, tomiodont length (*B*) can be calculated considering both the shortest (here right tomiodont length, *R*) and longest (here left tomiodont length, *L*) tomiodont lengths measured (Figure A2.3).

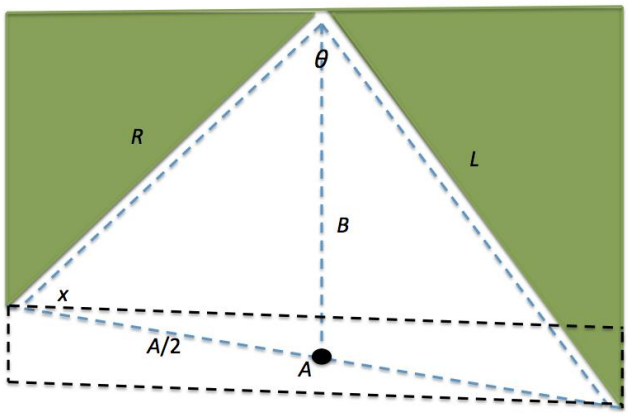

Figure 3: Diagrammatic frontal view of the tomiodonts of a Painted Turtle (*Chrysemys picta*). Line *B* represents the summary parameter tomiodont length, a measure of tomiodont length considering both the shortest (*R*) and longest (*L*) tomdiont lengths measured. *R* = right tomiodont length, *L* = left tomiodont length, *B* = tomiodont length, *A* = tomiodont gap width, *x* = angle contained between *R* and *A*, θ = tomiodont splay, angle contained between *R* and *L*.

Modify Eq. 1*b* for Triangle $RB\left(\frac{A}{2}\right)$ to solve for *B*:

$$B^2 = \frac{A}{2}\div^2 + R^2 \quad 2\ \frac{A}{2}\div R\ \cos(x) \qquad \textbf{(Eq. 2)}$$

Given that angle *x* remains unknown for Triangle $RB\left(\frac{A}{2}\right)$ and that Line *L* is known for Triangle *RLA*, substitute Eq. 1*a* into Eq. *b* to replace unknown angle *x* and simplify to solve for *B* (tomiodont length):

$$B^2 = \frac{A}{2}\div^2 + R^2 \quad 2\ \frac{A}{2}\div R\ \quad \frac{A^2 + R^2 \quad L^2}{2AR}\div \qquad \textbf{(Eq. 3}\text{, in progress)}$$

$$B^2 = \frac{A}{2}\div^2 + R^2 \quad AR\ \quad \frac{A^2 + R^2 \quad L^2}{2AR}\div \qquad \textbf{(Eq. 3}\text{, simplifying)}$$

$$B^2 = \frac{A}{2}\div^2 + R^2 \quad AR\ \quad \frac{A^2 + R^2 \quad L^2}{2AR}\div \qquad \textbf{(Eq. 3}\text{, simplifying)}$$

$$B^2 = \frac{A}{2}\div^2 + R^2 \quad \frac{A^2 + R^2 \quad L^2}{2}\div \qquad \textbf{(Eq. 3)}$$

Continue simplification to solve for *B* in Triangle $RB\left(\frac{A}{2}\right)$:

$$B = \sqrt{\frac{A}{2}\div^2 + R^2 \quad \frac{A^2 + R^2 \quad L^2}{2}\div} \qquad \textbf{(Eq. 4)}$$

Therefore, the summary parameter *B*, tomiodont length, is can be calculated using Eq. 4.

Appendix III: Qualitative evaluation of sexual dimorphism in head shape in *Chrysemys picta*

Accompaniment to Chapter I, section *Qualitative evaluation of head dimorphism*

Introduction

Qualitative evaluations of morphology for the identification of sex in the lab and field

For wildlife biologists, the ability to accurately identify a species, individuals within a population, and/or qualities of an organism (*e.g.*, sex) is essential for study. Colour, pattern, deformities and injuries, among other external features, may be reliable markers for the identification of individuals. Similarly, secondary sexual traits are obvious landmarks distinguishing the sex of study organisms.

Studies in the disciplines of (social) psychology and perception have examined the ability of human observers to correctly identify the sex of different animal species based on diagnostic features of the head or face. Observers were able to correctly differentiate the sex of Rhesus Macaques (*Macaca mulatta*) with 60.9% accuracy on the basis of sexually dimorphic traits of the face, including jaw size, nose size, eye size, face length and width (Franklin *et al*. 2013). The authors concluded that observers were capable of accurately sex-differentiating macaque faces by generalizing sexual dimorphisms found in human faces. Not surprisingly, in species with no obvious sexually dimorphic external characters, such as the Domestic Cat (*Felis domesticus*), participants performed poorly in identifying sex even with sex-identification training (Quinn *et al*. 1999). In contrast, Biederman and Shiffer (1987) found that with training, professionals could identify the sex of day-old chicks based on minute, although defining, characters

with >98% accuracy, illustrating the importance of instruction in training naïve observers to recognize identification landmarks.

In applied fieldwork, melon profile photographs of Bottlenose Whales (*Hyperoodon ampullatus*) have been used with high success to categorize individuals according to age-sex categories (female, immature male, subadult male, mature male) and produce results consistent with molecular sexing techniques (Gowans *et al*. 2000). Similarly, photographs of the sexually dimorphic dorsal fin in Bottlenose Dolphins (*Tursiops* sp.) have been used to non-invasively identify sex in the field (Rowe and Dawson 2009). From video recorded at migration monitoring stations, the sex of adult Chinook Salmon (*Oncorhynchus tschawytscha*) has been evaluated based on body proportions with up to 92% accuracy (Merz and Merz 2004).

Given the putatively sexually dimorphic nature of the head of Painted Turtles, cranial landmarks may serve in identifying the sex of individuals. A visual survey involving the sex identification of Painted Turtles based solely on cranial landmarks was conducted with the objective of testing if participants of differing experience levels are capable of accurately distinguishing female and male *C. picta* based on cranial landmarks. The survey tested the success of assigning sex based on visual examination of the head.

Objective

Recall that the objective of the research in Chapter I was to assess whether cranial morphology is sexually dimorphic in *Chrysemys picta*. As a complement to the quantitative analysis of measured traits (Chapter I), a visual survey was conducted to gauge whether there was a perceptible difference (as opposed to a simply statistically

demonstrable difference) in head morphology between female and male *C. picta*. Participants of varying experience levels are were asked to classify lateral head photos of female and male *C. picta* based on specified cranial landmarks. From this exploratory survey I propose that a perceptible difference in head morphology may be an important feature for sexual recognition (Legler 1990, Legler and Vogt 2013) or be a result of selective pressures on bite performance (Chapter I) in male *C. picta*.

Methods

Visual survey of cranial morphology

A visual survey involving the qualitative evaluation of Painted Turtle head morphology was conducted with participants of varying experience levels (Appendix IV). Participants were contacted via e-mail and provided with a generic background description of the survey, a Microsoft PowerPoint slideshow of the survey, and a Microsoft Excel answer sheet (Appendix IV). The survey audience was primarily composed of Laurentian University (Sudbury, Ontario, Canada) undergraduate and graduate students in biology, naturalist organizations, professional organizations (*e.g.*, Canadian Herpetological Society) and biology researchers (past and present) associated with the Algonquin Wildlife Research Station. Completed surveys were returned from participants that I did not contact directly, indicating that the survey was further distributed by participants.

In the self-guided survey, participants viewed slides of paired lateral photos of heads of mature (>100 mm midplastron length) Midland Painted Turtles (*Chrysemys picta marginata*) from Algonquin Provincial Park. Each slide showed a lateral view of two different adult turtles: one belonging to "Group A" (female) and one to "Group B"

(male). The biological significance (*i.e.*, sex) of the two groups was not revealed to participants. No turtle was used more than once in the survey. The placement of Group A and B photos on the left or right side of the screen was randomized.

Survey participants were provided with reference images with the three traits of interest identified for Group A and B turtles: rostrum length, tomiodont morphology, and overall head shape. Participants were then provided with three practice slides showing paired lateral head photos (as in the survey) to familiarize themselves with the format of the exercise. In these practice slides the "Group A" and "Group B" turtles were identified.

Before beginning the survey, participants were asked to identify their level of experience with Painted Turtles from four categories: novice, beginner, intermediate, or advanced. In Part I of the survey, participants were told to evaluate all three traits to best identify the "Group B" turtle in 25 photo pairings. In Part II, participants were again asked to evaluate all three traits to best identify the "Group B" turtle, but were also asked to specify which of the three head traits featured most prominently in their decision for each of the 26 photo pairings (for a total of 51 photo pairings). Following the visual comparison exercise, three supplementary questions were asked to gauge a participant's overall opinion on a difference in head structure between the groups, the most defining cranial landmark, and their general remarks regarding the survey (Appendix IV).

Statistical analyses

Visual survey of cranial dimorphism: All 51 lateral head photo pairings (from Parts I and II of the survey) were grouped and scored (/51) to evaluate the performance of participants in correctly identifying the sex of *C. picta*. A one-way ANOVA using

within-group weighted means was conducted to test for a difference in survey performance between participant experience levels followed by a Tukey's post-hoc test. The means of each group were weighted to account for unequal samples sizes between survey groups. In addition, a two-tailed exact binomial test evaluated whether participants of each experience level identified the correct sex of turtles at a level of significance above the chance percentage of 50%. That is, is the proportion of correct identification significantly higher than would be expected by chance? Answers to the supplementary survey questions were summarized and simply presented as descriptive statistics.

Results

Qualitative evaluation of cranial dimorphism

In total, 133 participants completed the Painted Turtle cranial morphology survey. Participants of all experience levels performed better than chance (50%) in identifying the sex of *C. picta* based on the three cranial landmarks ($p < 0.001$) (Figure A3.1). The distribution of survey scores for each level of experience show high performance across all experience levels with a mean score of approximately 80% (Table A3.1, Figure A3.2). A single participant in each of the beginner and intermediate experience levels was noted as an outlier (low score). Two participants, both in the advanced experience category, correctly distinguished the sexes in 100% of the photo pairings. Nonetheless, a marginally significant difference in the ability to discern sex of *C. picta* based on cranial morphology was found among experience levels ($F_{3,129} = 2.63$, $p = 0.053$). Post-hoc analysis showed that the mean score did not differ significantly between beginner,

intermediate and advanced levels of experience (Tukey's tests, $p > 0.05$ in all cases), although a significant difference was found between novice and advanced participants ($p = 0.030$) (Figure A3.1, Table A3.1).

Four participants identified an additional putative cranial dimorphism from their visual assessments. The slope of the "forehead", from anterior orbit to distal rostrum inclusive, was noted as regularly sloping in females from being highest at the orbit to lowest at the rostrum. In males this rostrum-orbit region is generally flat or horizontal (refer to Chapter I, Figure 1.4). Consistent across experience levels, participants identified overall head shape as the most defining cranial character (Table A3.2). Overwhelmingly, participants of all experience levels stated that there was a definitive difference in overall head shape and/or structure between male and female *C. picta* (Table A3.3). Participants at the novice and beginner experience levels demonstrate an approximately 10% higher acceptance of a definitive sex difference in overall head shape and/or structure compared to intermediate or advanced level participants (Table A3.3).

Discussion

Summary of findings

Cranial morphometric traits accurately distinguished adult females and males (conservatively ~80-85% accuracy). Rostrum length and tomiodont length were key traits distinguishing between the sexes, supporting my *a priori* anecdotal observations that these traits differed between the sexes. It is relevant that rostrum length and tomiodont length were included as landmarks in the cranial morphology surveys prior to the knowledge of statistical outcomes.

Survey results indicated that there are perceptible differences in cranial morphology between the sexes of *C. picta*. When observers were asked to classify a turtle as male or female they did so much better than predicted by chance. Regardless of a participant's level of experience with Painted Turtles, they accurately identified the sex of the turtle based on cranial morphology alone. Such findings provide strong support that there is a perceptible, rather than simply statistically demonstrable, difference in cranial structure between the sexes. The quantitative outcomes of the RMA and LDA analyses (Chapter I) are in agreement with the qualitative assessment conducted via the visual surveys.

Body shape, size, and recognition in chelonians

Several studies highlight the importance of visual cues in the mating behaviour of chelonians. In chelonians, body shape allows individuals to distinguish conspecifics, but does not appear inform about species or sex. For instance, male turtles will direct reproductive behaviours toward inanimate objects that resemble the body shape and size of conspecfics (Baker and Gillingham 1983, Hidalgo 1982). In addition, many interspecific and intrasexual chelonian sexual pairings have been reported (Eglis 1962, Davis and Jackson 1973, Baker and Gillingham 1983, Arndt 1986), suggesting that although body shape is a relevant signal for mate recognition, it likely functions alongside other cues (*i.e.*, tactical, chemical, and auditory; Liu *et al*. 2013).

Recall the dramatic bulbous snout and head dimorphism in some male Mesoamerican *Trachemys* taxa (see General Introduction). It has been proposed that the elongated snout may act in mate recognition or serve as an "erotic prod" (Legler 1990,

Legler and Vogt 2013). I propose that the dimorphic head structure of *C. picta* may also be related to mate recognition. Further, the angular head shape, pointed snout, and lengthened jawline of male *C. picta* may optimize bite force (Chapter II).

Conclusions

The research here, in addition to Chapter I, has demonstrated a statically and visually perceptible sexual dimorphism in head structure for *C. picta*. Human observers with varying levels of experience with *C. picta* were capable of distinguishing the sexes based on head morphology with a high degree of accuracy. Observers were also in agreement with the statement that there is a difference in overall head structure and/or shape between the two sexes. This difference in *C. picta* head shape may serve as a cue for sexual recognition within the species. Specific cranial landmarks, such as tomiodont and rostrum length, have application in the identification of individual sex in the field.

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Table A3.1: Summary statistics for score outcomes of Painted Turtle (*Chrysemys picta*) cranial morphometric trait surveys (n_{total} = 133) across the four levels of participant experience.

Level of experience	**N**	**Weighted mean score** (/51)	**Weighted mean score** (%)	**Range**	**Standard error**
Novice	31	40.06	78.55	25-49	0.91
Beginner	28	41.86	82.09	26-50	1.09
Intermediate	36	41.78	81.92	21-50	0.95
Advanced	38	43.71	85.71	31-51	0.83

Table A3.2: Summary of answers to closing survey question #1, "Of the three head characters, is there one that you found most defining?" Answers expressed as a percentage that the trait was named as the primary or defining character for the decision to classify a *Chrysemys picta* lateral head photo as Group A (female) or Group B (male). Percentages may not total 100% because of rounding.

	Most defining cranial landmark?		
Level of Experience	**Rostrum length** (%)	**Overall head shape** (%)	**Tomiodont morphology** (%)
Novice	28.71	39.10	32.18
Beginner	29.12	41.90	28.98
Intermediate	31.84	39.64	28.53
Advanced	35.43	39.17	25.40

Table A3.3: Summary of answers to closing survey question #2, "Considering all three characters [rostrum length, overall head shape, and tomiodont morphology], do you feel that there is a difference in overall head shape and/or structure between 'Group A' and 'Group B' turtles?" Answers of survey participants were interpreted for placement in one of five categories describing the overall head morphology of Algonquin Provincial Park Midland Painted Turtles (*Chrysemys picta marginata*): no definitive difference, small degree of difference with few exceptions, undecided, high degree of difference with few exceptions, and lastly, a definitive difference in cranial morphology between Group A (female) and Group B (male) *C. picta*.

	"Difference in overall head shape and/or structure?"				
Level of experience	**No, definitively**	**No, with exception**	**Undecided**	**Yes, with exception**	**Yes, definitively**
Novice	3	1	1	3	23
Beginner	1	0	1	6	20
Intermediate	1	2	4	7	22
Advanced	2	0	7	4	25

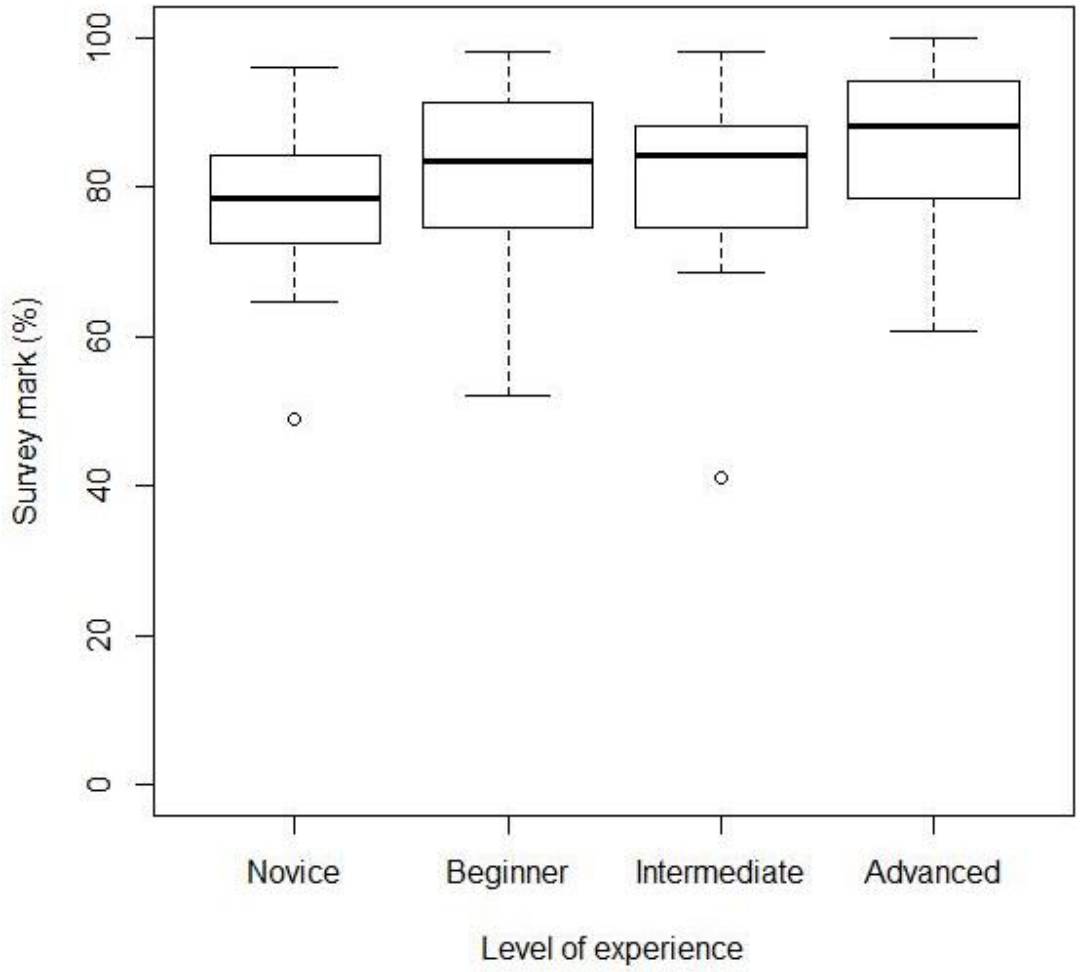

Figure A3.1: Scores from Painted Turtle (*Chrysemys picta*) cranial morphology survey involving participants of varying experience levels. Box delineates the 25th and 75th quartiles, median as weighted line, whiskers extend to the maximum and maximum values of the dataset, and the hollow circles represent outliers.

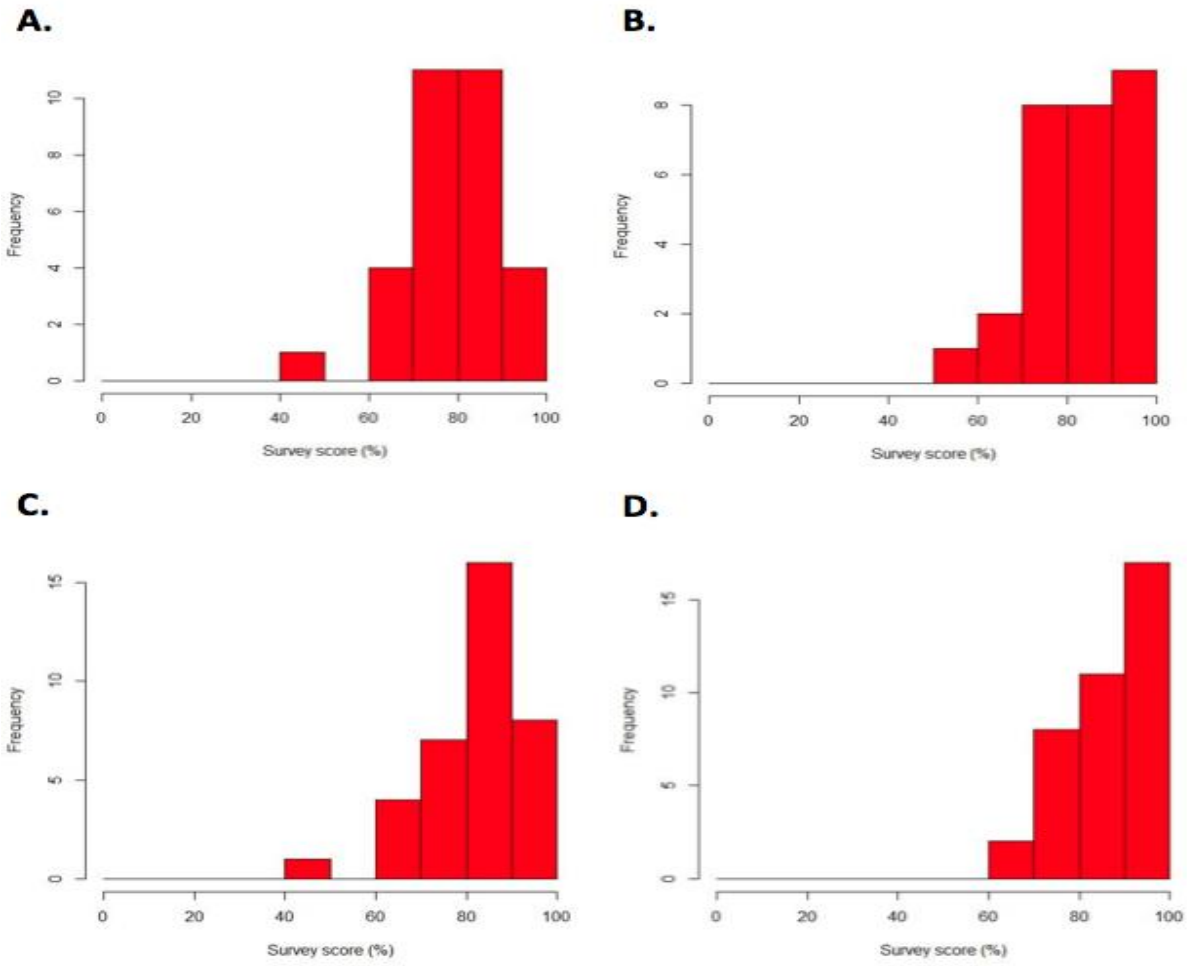

Figure A3.2: Histogram of survey score (expressed as percentage) across four levels of participant experience; novice (A), beginner (B), intermediate (C), and advanced (D). Note that frequency scales with different values between plots.

Appendix IV: Background information related to visual head morphology survey

Accompaniment to Appendix III, Methods, *visual survey of cranial morphology*

As part of Appendix IV please refer to the Microsoft PowerPoint survey slideshow entitled, "Categorization of Midland Painted Turtles (*Chrysemys picta marginata*) according to head morphology" and Microsoft Excel answer spreadsheet, both provided as external files.

Every e-mail participant request was accompanied by the generic message (below) providing survey background and introductory information. The message below was accompanied by a 68-slide Microsoft PowerPoint slideshow containing survey instructions (written and visual), turtle photo pairings, supplementary survey questions and author contact information (refer to Chapter I, Methods, *Visual survey of cranial morphology*, for further details). The message was also coupled with a Microsoft Excel spreadsheet in which participants could record their answers. Completed surveys were conducted with anonymity and were returned via e-mail.

Subject: Painted Turtle head morphology – research participant request

I am kindly asking for your participation in a survey I am holding as part of my research. Please note that this exercise will take approximately 30 minutes to complete and must be completed in one sitting. The survey is treated anonymously and to be conducted individually. I understand if you are unable to participate due to time constraints, *etc*.

The objective of this survey is to see if there is a visible difference in the head structure (morphology) among groupings of Algonquin Painted Turtles. This past summer I took lateral head photos of "Group A" and "Group B" Painted Turtles. In setting up this exercise I have paired head photos of "Group A" and "Group B" turtles on a single slide. Participants will evaluate three physical characters (rostrum length, tomiodont morphology and overall head shape; each explained in the slideshow) to gauge the validity of these characters in defining a group.

In the attached slideshow you will find the instructions and photos that accompany this

exercise. There is also a spreadsheet in which to type your answers. Both the slideshow and spreadsheet will need to be accessible during the exercise.

Feel free to distribute this message to others (friends, partner, colleagues, naturalists, biologists and even non-nature minded folks!) that may be willing to participate. For those interested in participating I would appreciate a brief confirmation e-mail so that I keep a participant tally. A 1-2 week period to complete the survey would be preferred.

Please let me know if you encounter any difficulties or have any questions. Thank you very much for your time and consideration,

Patrick Moldowan
MSc. Biology candidate
Laurentian University
Sudbury, Ontario
Canada
pmoldowan1@laurentian.ca

Supplementary survey questions

After the visual comparison exercise was complete, participants were asked three questions pertaining to their overall impression of the exercise: 1) "Of the three head characters, is there one that you found most defining? Please specify one trait (rostrum length, overall head shape and tomiodont morphology), additional comments welcomed"; 2) "Considering all three characters, do you feel that there is a difference in overall head shape and/or structure between 'Group A' and 'Group B' turtles" (yes/no) and; 3) "Any general comments or feedback". See survey directly for format details.

Appendix V: *In situ* observations of male-female Midland Painted Turtle (*Chrysemys picta marginata*) antagonism

Accompaniment to Chapter III, Introduction, *Reproductive tactics and reports of male-female antagonism in Chrysemys picta*

Table A5.1: *In situ* observations of male-female Midland Painted Turtle (*Chrysemys picta marginata*) antagonism in Algonquin Provincial Park. Alphanumeric and numeric codes represent individual turtle identification codes. Arowhon population locales are represented as Wolf Howl Pond (WHP) and Wolf Howl Pond East (WHPe). Note that Broadwing Lake (Broadwing) is not part of the Arowhon population. Observations from 2000-2004 compiled by E. Hughes, observations from 2013 compiled by P. Moldowan.

Date	Location	Time	Observation
04/05/2000	WHP	10:00	Male (ID E01 tag) biting female (ID Z01 tag)
20/05/2000	WHP	10:30	Male (ID X36 tag) biting female (ID J13 tag), they were positioned face-to-face
20/05/2000	WHP	13:00	Male (ID X05 tag) observed biting the neck of female (ID B39 tag) at the surface of the water. They are partially suspended in mud extending from a bog mat. The female drew her head within her carapace and the male extended his neck such that his head disappeared within the female's carapace. The duration of biting lasted approximately 10 minutes. Upon examining the female, the skin was broken and pinched together, making it obvious where the male had been biting her.
07/06/2000	WHP	14:40	Female (ID X24 tag) was observed biting the carapace of male (ID A01 tag). The turtles were positioned at the surface of the water in mud extending from a bog mat and both were nearly flipped on their backs. The male had pulled his head deep within his carapace.
06/05/2001	WHP	*NA*	Three independent incidents of unidentified males biting, chasing and courting unidentified females.
13/05/2001	WHP	13:00	Male (ID C34 tag) was trying to bite the head of female (ID A50 tag). The female's head was retracted into her shell. Male C34 oriented his head between A50's carapace and plastron (to the point that only his neck was visible). He did not make any attempt to bite the female's forelimbs. When male C34 succeeded in biting the female on the neck, he rotated such that the plastron of the female was

			visible. Biting lasted approximately 3 minutes, after which they were caught in a dip net. The researcher was unable to separate the turtles.
17/05/2002	WHP	14:00	Male (ID 0336 tag) attempted to bite dorsal neck of female (ID 0334 tag).
06/2004	WHP	*NA*	Male (ID N14 tag) observed biting female (ID B26 tag) on the neck. Biting lasted approximately 10 minutes during which time there were periods of violent struggling. The male attempted to pull the female's head out from a retracted position. The researcher could hear audible shell clattering and during the approximately 5 min the turtles were at the water surface they created surface disturbance and wake. Female B26 appeared to be experiencing pain (limbs immobile, mouth open) and demonstrated resistance. Both turtles sunk to rest on the substrate. The end of the biting episode was not observed. Female B26 was recaptured approximately 5 min later. On inspection, there were no visible marks on her neck at the bite location.
08/05/2013	Broadwing	10:50	Male (ID 0950 notch) biting female (ID 163 tag, 0116 notch) on right lateral neck. Male first observed on muddy substrate and appeared to be foraging. Researcher (M. Keevil) swept with dip net and recovered the male biting a female on the right lateral neck. Male maintains hold on female for 2 minutes following netting and an additional 30 seconds in hand before the pair was separated. Male demonstrates multiple shaking and jerking motions while biting female and attempts shell clattering behaviour. Female completely retracted into shell and immobile throughout biting episode Despite bite, female did not bear an external wounds on later inspection [Appendix VII, Video A.8].
26/05/2013	WHPe	Not noted	Male (ID 1630 tag) struck at anterior carapace and head of female (ID 2912 notch) in open water, male did not make contact, female promptly dove and swam away.
27/05/2013	WHPe	1135	Male (ID 1082 tag) biting nape of female (ID F06 tag, 0023 notch) and pinning her to substrate on shallow bog mat shelf, both turtles completely submerged, female did not demonstrate fresh wounds upon separation and inspection.
08/08/2013	WHP	2005	Male (ID 184 tag) biting throat of female (ID tag

	A13), male continued to maintain hold of female for greater than 1 minute following netting and handling. Female demonstrated puckered but unbroken skin along left symphyseal stripe (throat) at bite site. Researcher (P. Moldowan) alerted to interaction from audible commotion in water, splashing and shell clattering ("hollow knocking sound") heard from a distance of ~3m [PHOTOGRAPH of female wound].

Appendix VI: Reproductive behaviour ethogram of *Chrysemys picta*

Accompaniment to Chapter III, Methods, *Ethogram development and behavioural trial review*

The ethogram used in the evaluation of *C. picta* reproductive behaviour is derived from the work of Jackson and Davis (1972), Baker and Gillingham (1983), Kramer (1984, 1986, 1989*a*,*b*), Thomas (2002), Pandav *et al*. (2007), and Davis (2009). Context categories represent neutral (non-aggressive, non-display sexual interaction), courtship (non-aggressive, display sexual interaction) and coercive (aggressive, display sexual interaction) behaviours.

Behaviour*	Definition	Context
Approach	Directed movement toward conspecific through shift in orientation or trajectory	Neutral
Bite (body)	Grasping of exposed limbs, tail or shell with closed jaws	Coercive
Bite (head)	Grasping skin of the head or neck of with closed jaws	Coercive
Charge	Aggressive frontal approach involving rapid swimming toward conspecific, may be accompanied by open-mouth gape	Coercive
Chase	Following initial contact two individuals, one rapidly pursues the fleeing conspecific	Coercive
Cloacal sniff	Investigation of the tail, cloaca, or posterior regions of the shell; extension of head toward tail or inguinal region; trailing a conspecific	Neutral
Copulation	Intromission of penis into the female cloaca	Neutral
Forced submergence	Male pinning of the female underwater through coercive action (*e.g*., biting and shell clattering) for greater than 30 seconds	Coercive
Foreclaw display	Rhythmic display of the foreclaws between mature or immature turtles in intrasexual pairings, not of reproductive context (Thomas and Altig 2006). Also see Titillation.	Neutral

Mount	Male approaches from behind, female carapace-male plastron contact, positioning vents in alignment, female immobile.	Neutral
Shell clattering	Rapid and repeated extension and retraction of the male's neck during biting resulting in the shell of the male and female knocking together (Kramer 1984, 1989)	Coercive
Strike	Open mouth gaping and lunging at exposed limbs, shell, or head; head thrust forward with the jaws open, but jaws do not close shut. A strike may be directed from one of four orientations: • Dorsal: male approaches or is positioned behind female, male swims or climbs over carapace, and strikes at dorsal head or neck • Ventral: male approaches or is positioned behind female and dives underneath female, male resurfaces and strikes at the throat and ventral neck of the female • Lateral: male approaches or is positioned beside female and strikes at the lateral head or neck of female • Frontal: male approaches or is positioned in front of female and initiates a strike while the pair is face-to-face	Coercive
Titillation	Rhythmic display of the foreclaws by males directed at females, digits of male forelimbs vibrated rapidly against a female turtle's head, used exclusively in courtship (Kramer 1989, Thomas and Altig 2006)	Courtship

*Note that two previously-defined behaviours, Dragging and Yanking, were excluded from the ethogram due to difficulty in observation and quantification from the video recordings. Dragging was defined as a change in position as a result of either biting or being bitten by another turtle (Kramer 1989). Yanking was defined as a turtle vigorously pulling on the bite site while pushing or holding the conspecific's shell away with its front legs (Kramer 1989), resulting in behaviours similar to those defined for Shell clattering.

Open mouth gaping (Bury *et al*. 1979) was observed during male-male, male-female, and female-female interactions, although video recordings did not provide high enough resolution to distinguish this behaviour consistently. Future studies may wish to quantify this behaviour because it is no doubt relevant for interactions between individuals.

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Appendix VII: Video recordings of notable male *Chrysemys picta* reproductive behaviours during spring and late summer trials, Arowhon population, Algonquin Provincial Park.

Accompaniment to Chapter III, Results, *Description of male aggression and shell clattering behaviour*

Video A.1: Trial 7, Spring. Male ID 1424 notch, females IDs B07 tag, 182 tag, and 2912 notch. Male *C. picta* 1424 notch titillates female B07 tag.
https://www.youtube.com/watch?v=czVRe6hzLzg&feature=youtu.be

Video A.2: Trial 11, Spring (Incomplete trial). Male ID E13 tag, female IDs 24 tag, 147 tag, and 1627 notch. Male *C. picta* E13 tag bites female 24 tag at onset of trial and author (P. Moldowan) remains in immediate vicinity to document behaviour. Male displays biting, forced submergence, and shell clattering. See Figure 3.5 of photos of male biting and female injury taken during Trial 11, Spring.
http://www.youtube.com/watch?v=2724UNaYyLE

Video A.3: Trial 24, Spring. Male ID E13 tag (redo of incomplete Spring Trial 11 with male E13 tag), female IDs A41 tag, B32 tag, and 156 tag. Male *C. picta* E13 tag bites female 156 tag, followed by forced submergence and shell clattering. At trial completion (2 hours), the author (P. Moldowan) visits trial to release turtles and begins documenting coercive male behaviour.
https://www.youtube.com/watch?v=ykeMHio88io&feature=youtu.be

Video A.4: Trial 3, Late Summer. Male ID 188 tag, female IDs A38 tag, C48 tag, and 1106 tag. Male *C. picta* 188 tag bites female A38 tag and engages in shell clattering. Female A38 tag displays strong resistance, including open mouth gaping, struggling, flailing of her forelimbs, and backward swimming.
https://www.youtube.com/watch?v=ofoOKn1GJd4

Video A.5: Trial 4, Late Summer. Male ID 1078 tag, female IDs 155 tag, 618 tag, and 1203 tag. Male *C. picta* 1078 tag approaches and initiates titillation with female 155 tag.
https://www.youtube.com/watch?v=ScbLFirUrZY&feature=youtu.be

Video A.6: Trial 18, Late Summer. Male ID 197 tag, female IDs B13 tag, 1076 tag, and 1184 tag. Male *C. picta* 197 tag bites female 1184 tag at onset of trial and author (P. Moldowan) remains in immediate vicinity to document behaviour.

A.) Above-water video recording of male 197 tag biting, forced submsergence, and shell clattering of female 1184 tag.
https://www.youtube.com/watch?v=CEwS9dl0Cc0&feature=youtu.be

B.) Underwater video recording. While biting, male appears to drag female in open water. Female demonstrates resistance by outstretching forelimbs to shield from male's shell clattering. Male uses his forelimbs in an attempt to clear the obstructive forelimbs of the female. Shell clattering audible.
https://www.youtube.com/watch?v=LM2MzCAWE20&feature=youtu.be

C.) Underwater video recording. Additional recording of male shell clattering. Male Audible shell clattering.
https://www.youtube.com/watch?v=s3WkxkiDuaM&feature=youtu.be

D.) Underwater video recording. Male initiates shell clattering from resting position on the substrate. Audible shell clattering.
https://www.youtube.com/watch?v=DRbKvWESUQM&feature=youtu.be

Video A.7: Trial 22, Late Summer. Male ID 811 tag, female IDs B05 tag, 182 tag, and 601 tag. Male *C. picta* 811 tag approaches and bites female 182 tag from ventral position. Male engages in an extended period of biting and forced submergences with frequent shell clattering.
http://www.youtube.com/watch?v=UJbThn0mGhY

Video A.8: *In situ* observation and recording of biting and attempted shell clattering by male *C. picta*, Broadwing Lake, Algonquin Provincial Park. Male *C. picta* (ID 0950 notch) biting female (ID 163 tag, 0116 notch) on right lateral neck. Video recording made following capture of the pair**.** See Table A5.1 for additional information. Recording by M. Keevil.
https://www.youtube.com/watch?v=2KjHOQ-qrig&feature=youtu.be